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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Fisheries and Oceans
Pêches et Océans

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Printed in Canada by: The Runge Press Limited, Ottawa

Imprimé au Canada par: The Runge Press Limited, Ottawa

Design: Ludvic Saleh & Associates, Ottawa

Conception graphique: Ludvic Saleh & Associates, Ottawa

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937 et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–1979.

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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 45, No. 5, May 1988

Volume 45, nº 5, mai 1988

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Reproductive Capacity of Dragraked and Non-Dragraked Irish Moss (*Chondrus crispus* Stackhouse) Beds in the Southern Gulf of St. Lawrence

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Chopin, T., J. D. Pringle, and R. E. Semple. 1988. Reproductive capacity of dragraked and non-dragraked Irish moss (*Chondrus crispus* Stackhouse) beds in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 45: 758–766.

A non-dragraked bed of *Chondrus crispus* Stackhouse (Rustico) showed a greater year-round carposporangial reproductive capacity than a dragraked bed (Miminegash). The former had a lower frond density but larger fronds which were the major sources of reproduction. Although carposporangial sori had a greater area and were more frequently full in Miminegash, reproductive capacity was higher in Rustico due to higher sorus densities per frond and sample unit. All the studied parameters did not show significant ($P = 0.05$) differences between the study sites for tetrasporophytes, resulting in similar overall tetrasporangial reproductive capacities. Reproductive capacity peaked in Miminegash prior to the harvesting season. Class 4 and 5 fronds (largest fronds) have the greatest reproductive capacity. To protect this source of spores and thus improve bed reproductive potential, a 1-mo delay in the present season opening date is suggested. The much higher tetrasporophyte reproductive capacity over that of carposporophytes is at least a partial explanation for the greater gametophytic abundance in some populations.

La capacité de reproduction des carposporocystes de *Chondrus crispus* Stackhouse est plus importante tout au long de l'année dans un champ inexploité (Rustico) que dans un autre, exploité par des dragues à râteaux (Miminegash). Le premier a une densité de frondes inférieure mais possède des plantes plus développées qui contribuent à la plus grande part de la reproduction. Bien que les carposporocystes aient une surface plus grande et soient plus souvent pleins à Miminegash, leur capacité de reproduction est plus importante à Rustico en raison de leur plus grande densité par fronde et par unité d'échantillonnage. Aucune différence significative ($P = 0,05$) n'est observée dans les paramètres étudiés pour les tétrasporophytes, ce qui conduit à une égale capacité de reproduction globale des tétrasporocystes dans les deux sites. Cependant, cette dernière possède un grand potentiel à Miminegash avant que la saison de pêche débute. Les frondes les plus développées (classes 4 et 5) possèdent la capacité de reproduction la plus importante. Comme aucune technique de récolte ne peut préserver ces individus, un délai d'un mois de la date actuelle d'ouverture de la saison de pêche est suggéré pour améliorer le potentiel de reproduction des champs. La plus grande capacité de reproduction des tétrasporocystes, par comparaison aux carposporocystes, peut expliquer en partie la prédominance gamétophytique de certaines populations.

Received July 23, 1987
Accepted January 7, 1988
(J9366)

Reçu le 23 juillet 1987
Accepté le 7 janvier 1988

The perennial red alga *Chondrus crispus* Stackhouse (Irish moss) is the basis of an important marine plant fishery in the Canadian Maritime Provinces (MacFarlane 1964; Ffrench 1971; Pringle 1976). Traditionally, it has been the second most valuable fishery, after lobster, on Prince Edward Island (Anonymous 1985). The crop is processed for carrageenans, colloids whose gelling, thickening, and stabilizing properties are used in industries such as food processing, pharmaceuticals, and cosmetics (Chopin 1986).

Problems in maintaining a stable annual yield began in 1971 in Marine Plant Harvesting District (MPHD) 1 (Fig. 1), the most productive Irish moss stock in the northwestern Altantic (Pringle 1981). Annual yields decreased following an increase in both fishing pressure (Pringle and Semple 1984) and fishing power without a concomitant resource management plan (Pringle 1986). Resource abundance controlled annual yields (Pringle 1981), and mean frond weight was significantly less than in other districts (Pringle and Sharp 1986), suggesting growth overharvesting. Furthermore, Pringle and Semple (1984) noted patches of prime substrata (sandstone ledge), barren of macrophytes. These areas in some commercial dragraked beds represented up to 21% of the ledge and have persisted for up to 7 yr (unpublished data). Pringle and Semple (1984) hypothesized that this long-term condition was the result of recruitment overharvesting.

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Considerable information has been published on *C. crispus* reproductive phenology in France (Kopp 1975; Chopin 1986), in New England (Prince and Kingsbury 1973; Mathieson and Burns 1975), and in the Canadian Maritime Provinces (MacFarlane 1968; Bhattacharya 1985). However, data are unavailable on *C. crispus* reproductive capacity. The present study was designed to obtain quantitative data on aspects of reproduction in southern Gulf of St. Lawrence *C. crispus* beds. We test in particular the null hypothesis that the reproductive capacity is not significantly ($P = 0.05$) different between a commercial dragraked bed (Miminegash) and a commercially important non-dragraked bed (Rustico; fronds are cropped via wave shock and ice scouring and harvested as "storm toss" (Pringle and Mathieson 1986)).

Materials and Methods

Reproductive capacity of *C. crispus* in defined here as the sorus area per unit area (0.25 m^2) of ocean bottom over a 12-

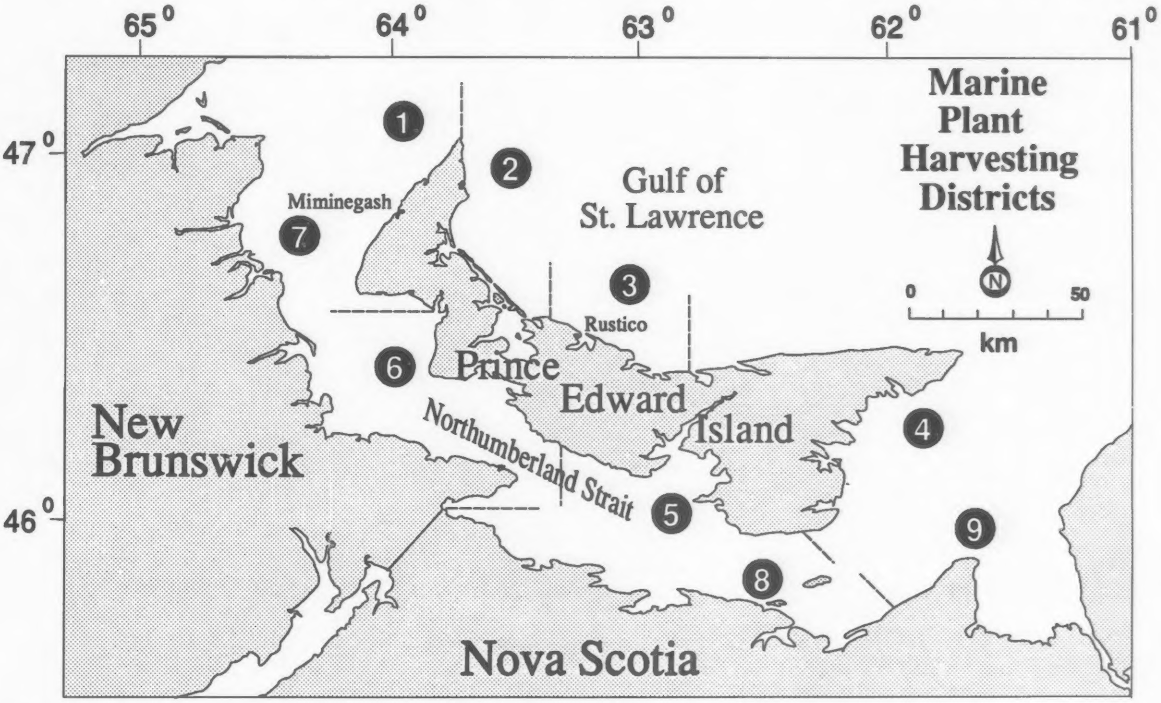

FIG. 1. Location of the studied *Chondrus crispus* beds in Prince Edward Island, Canada: Miminegash (MPHD 1, dragraked) and Rustico (MPHD 3, non-dragraked).

TABLE 1. Mean density and percentage of fronds per 0.25 m^2 of the different frond classes in Miminegash (M) and Rustico (R). Asterisks indicate significant ($P \leq 0.05$) differences between the two locations.

	Class 1		Class 2		Class 3		Class 4		Class 5		All classes	
	M	R	M	R	M	R	M	R	M	R	M	R
Density of fronds·0.25 m^{-2}	163.9*	69.8*	341.8*	274.3*	94.2*	73.4*	72.1*	97.1*	27.4	30.1	699.5*	544.7*
Density of carposporangial fronds·0.25m^{-2}			3.9*	6.1*	4.0	4.0	6.5*	15.1*	3.9*	7.8*	18.3*	33.0*
Density of tetrasporangial fronds·0.25 m^{-2}			3.3	2.5	4.4*	2.4*	10.7	11.0	4.1	4.2	22.6	20.1
Dry weight (g) of fronds·0.25 m^{-2}	0.81*	0.32*	9.37	8.07	7.37*	5.18*	13.61*	19.60*	10.20*	15.44*	41.36*	48.62*
Dry weight (g) of carposporangial fronds·0.25 m^{-2}			0.20*	0.35*	0.41	0.37	1.40*	3.91*	1.67*	5.10*	3.68*	9.73*
Dry weight (g) of tetrasporangial fronds·0.25 m^{-2}			0.19	0.15	0.54*	0.25*	2.69	3.04	2.22	2.72	5.64	6.17

mo period. Reproductive capacity was calculated from the following parameters: frond density, frond biomass and number, and area and state of fullness of sori per frond. Samples were collected from beds at Miminegash (Cape Cage and Pleasant View reefs, which have been dragraked yearly from approximately 1958) and Rustico (Orby Head; Fig. 1). The latter bed was dragraked only during 1969 and 1970; dragraking was banned in 1971 (Craigie and Pringle 1978). Collections were made monthly during spring and summer and bimonthly thereafter. Dynamic ice conditions did not permit a January Miminegash collection. Three transects running perpendicular to the shore through the *C. crispus* beds were established at each site. Three stations (inner, middle, and outer) were designated on each transect. Three sample units were haphazardly chosen at each station (thus, $n = 27$) by dropping a quadrat frame of 0.25 m^2 (that size deemed most efficient by Pringle (1984)) from the diver tender. All macroalgae in each quadrat were hand-collected by divers and carefully placed in a fine-mesh sampling bag. The samples were transferred to plastic bags, stored in a cooler on the boat, and later (no more than 5 h) frozen at −30°C until sorting. The method of frond removal underestimates Class 1 frond density (frond class characteristics are given below). However, the impact will be nil on reproductive capacity estimates, as these fronds do not sporulate (J. D. Pringle, unpubl. data).

The plants in a sample (combination of all sample units per site per collection) were initially separated into three categories: (1) entire fronds of *C. crispus*; (2) torn pieces (''torns'') of *C. crispus*; and (3) ''other'' algae. Torn pieces, representing only 9.7 and 11.7% of the total biomass of *C. crispus* at Miminegash and Rustico, respectively, were not included in reproductive capacity estimates, as their origin was unknown. *Chondrus* fronds were placed in one of five classes, based on number of dichotomies and frond length, using a slightly modified version of the classification of Sharp et al. (1986): Class 1 = nondichotomous fronds; Class 2 = fronds with up to three dichotomies and a frond length less than 10 cm, or fronds with any number of dichotomies and a frond length less than or equal to 6 cm; Class 3 = fronds with four or five dichotomies and a frond length between 6 and 10 cm; Class 4 = fronds with more than five dichotomies and a frond length between 6 and 10 cm; Class 5 = fronds with any number of dichotomies and a frond length greater than 10 cm.

Fronds within each class were sorted into three groups: (1) reproductive female gametophytes; (2) reproductive tetrasporophytes; and (3) non-reproductive fronds (which, on occasion, included mature male gametophytes). The number of fronds in each group was determined. Up to 10 specimens were haphazardly chosen from each of the first two groups; the number of sori per frond and their state of fullness (a subjective assessment using the following categories: empty, partially empty, and full) were determined for each individual. One sorus per chosen frond was subjectively assessed as a ''typically sized'' sorus for that frond, and its area (A) was determined. Frond reproductive capacity (FR) per frond class per reproductive type per study site (carposporangial or tetrasporangial) was determined as follows:

(1) $\mathrm{FR} = A \cdot \mathrm{So}$

where So is the number of sori. Mean frond reproductive capacity was then calculated

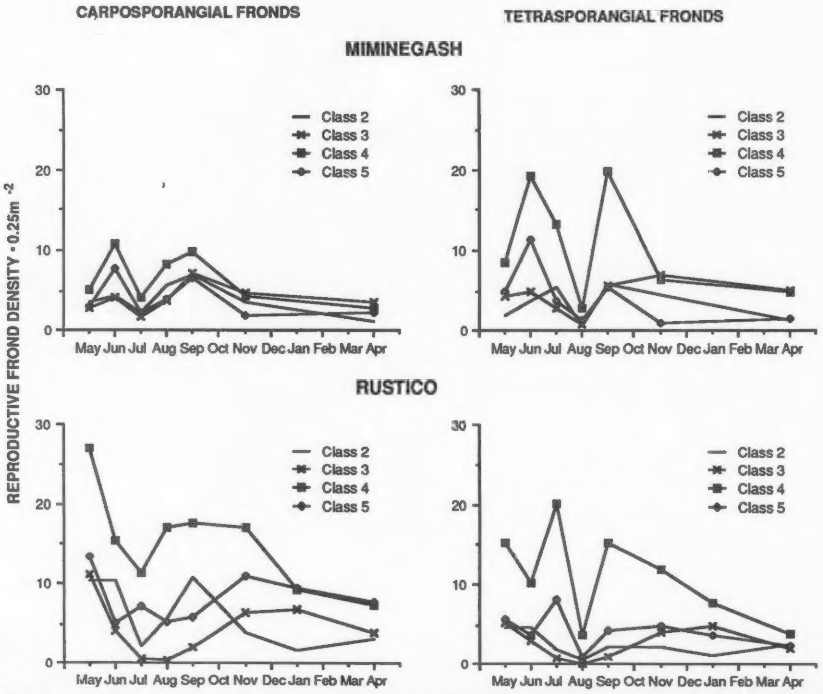

FIG. 2. Density of carposporangial and tetrasporangial fronds from May 1985 to April 1986 at Miminegash and Rustico.

TABLE 2. Mean sorus density per frond and per 0.25 m² of the different frond classes in Miminegash (M) and Rustico (R). Asterisks indicate significant ($P \leq 0.05$) differences between the two locations.

	Class 2		Class 3		Class 4		Class 5		All classes	
	M	R	M	R	M	R	M	R	M	R
Density of carposporangial sori·frond^{-1}	16.9*	22.1*	23.1	23.7	52.6*	86.7*	76.6*	190.2*	42.3*	80.7*
Density of tetrasporangial sori·frond^{-1}	42.0	43.1	63.3	73.9	145.9*	180.1*	295.1*	428.1*	136.6*	181.3*
Density of carposporangial sori·0.25 m^{-2}	79.3*	165.8*	103.8*	143.2*	386.3*	1431.8*	384.6*	1658.4*	974.4*	3406.8*
Density of tetrasporangial sori·0.25 m^{-2}	164.4	150.2	319.9	297.1	1953.6	2192.2	2181.1	2118.1	5022.8	4775.9

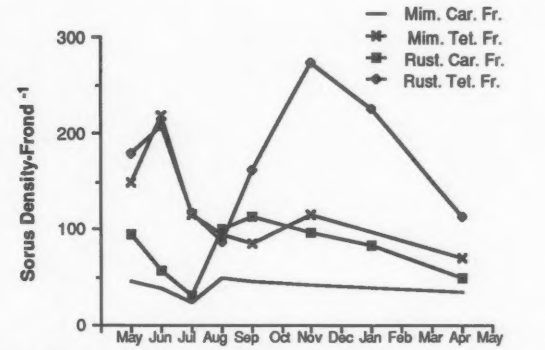

FIG. 3. Sorus density per frond from May 1985 to April 1986. Mim., Miminegash; Rust., Rustico; Car., carposporangial; Tet., tetrasporangial; Fr., frond.

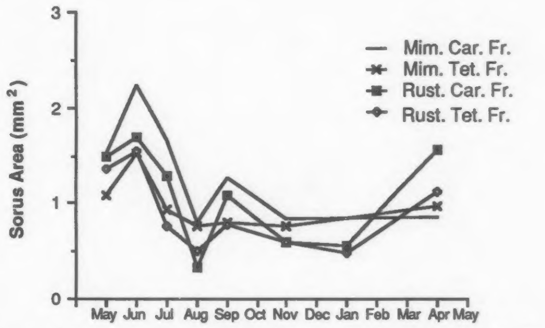

FIG. 4. Sorus area from May 1985 to April 1986 (see Fig. 3 for abbreviations).

$$(2) \quad \langle FR \rangle = \sum_{i=1}^{i\leq 10} FR/No$$

where No is the number of selected fronds (≤ 10). Sample unit (Su) reproductive capacity per class was determined with the following:

$$(3) \quad SuR = \langle FR \rangle \cdot Cl$$

where Cl is the total number of fronds per class in the respective sample unit. Mean sample (Sa) reproductive capacity per frond class was calculated

$$(4) \quad \langle SaRCl^{-1} \rangle = \sum_{i=1}^{i=27} SuR/n'$$

where n' is the number of sample units (≤ 27). Mean sample reproductive capacity was determined as follows:

$$(5) \quad \langle SaR \rangle = \sum_{i=C12}^{i=C15} \langle SaRCl^{-1} \rangle.$$

Mean annual (An) reproductive capacity was calculated with the following formula:

$$(6) \quad \langle AnR \rangle = \sum_{i=1}^{i=8} \langle SaR \rangle / n$$

where n is the number of samples. This procedure was followed for each frond class of both reproductive types. The biomass of each frond class was determined by heating the fronds at 80°C for 72 h.

Usual statistics (mean, standard deviation, etc.), normality, and regression analyses were carried out with packaged computer programs (Nie et al. 1975). All distributions were normal; thus, the parametric Student t-test was employed to determine significant differences ($P \leq 0.05$) between means. Percentages were transformed in arcsin to permit statistically significant ($P \leq 0.05$) differences to be delineated (Sokal and Rohlf 1969).

Results

Frond Density

Chondrus crispus total frond density per 0.25 m² was significantly greater in Miminegash (699.5) than in Rustico (554.7) (Table 1). There were significantly more Class 1, 2, and 3 fronds in Miminegash but more Class 4 fronds in Rustico. The mean number of Class 5 fronds was not significantly different between the two locations.

The density of carposporangial and tetrasporangial fronds (referred to hereafter as "mature" or "fruiting") throughout the study period exhibited a bimodal pattern at both locations, with maxima in early summer and autumn (Fig. 2). Minima for the former occurred in early spring and July, and for the latter in August. Reproductive Class 4 fronds at both locations had the highest densities amongst the spore-bearing classes. There were significantly more Class 2, 4, and 5 carposporangial fronds in Rustico than in Miminegash (Table 1) but more mature Class 3 tetrasporophytes at the latter site. Overall, carposporangial

TABLE 3. Mean sorus area and reproductive capacity of the different frond classes in Miminegash (M) and Rustico (R). Asterisks indicate significant ($P \leqslant 0.05$) differences between the two locations.

	Class 2		Class 3		Class 4		Class 5		All classes	
	M	R	M	R	M	R	M	R	M	R
Carposporangial sorus area (mm^2)	1.14*	1.03*	1.36*	1.15*	1.28*	1.13*	1.56*	1.16*	1.33*	1.12*
Tetrasporangial sorus area (mm^2)	0.86*	0.97*	1.00	0.95	1.08*	1.01*	1.22*	0.97*	1.04	0.97
Carposporangial reproductive capacity (mm^2·0.25 m^{-2})	88.57*	174.37*	143.11	152.49	538.47*	1486.62*	728.13*	1761.35*	1498.28*	3574.83*
Tetrasporangial reproductive capacity (mm^2·0.25 m^{-2})	154.18	172.97	348.24*	245.09*	2438.58	2186.75	3047.81*	1888.76*	5988.81	4493.57

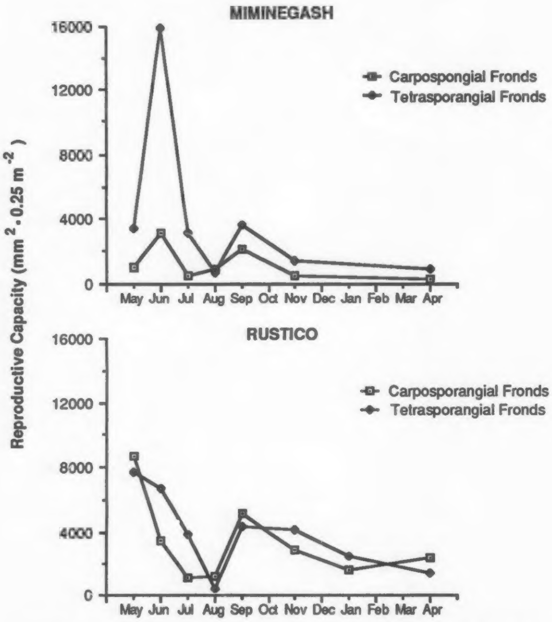

FIG. 5. Reproductive capacity from May 1985 to April 1986 at Miminegash and Rustico.

fronds were 1.8 times more dense at Rustico (33.0) than at Miminegash (18.3), but the density of mature tetrasporophytes at the two sites was not significantly different (20.1 and 22.6, respectively). The overall percentage of reproductive fronds was always low. Carposporangial fronds were 2.3 times more frequent in Rustico (6.1%) than in Miminegash (2.6%). However, the frequency of mature tetrasporophytes between the two sites was similar (3.7 and 3.2%, respectively).

Frond Biomass

The overall mean biomass was significantly greater in Rustico (48.62 g) than in Miminegash (41.36 g) (Table 2) due to significantly greater densities of larger fronds in Rustico. Annual variations in biomass of both carposporangial and tetrasporangial fronds followed a similar pattern ($r = 0.87$) to that of frond density (Fig. 2). Biomass of each of Class 2 and 3 fronds was always much lower than that of each of Classes 4 and 5 fronds, except in autumn and winter in Miminegash. The biomass of Class 2, 4, and 5 carposporangial fronds was significantly greater in Rustico than in Miminegash; the reverse was the case for Class 3 tetrasporangial fronds (Table 1). Overall, the mean biomass of carposporangial fronds per 0.25 m^2 was 2.6 times greater in Rustico (9.73 g) than in Miminegash (3.68 g). There was no significant difference in the biomass of tetrasporangial fronds between sites. The percentage contribution of reproductively mature Class 2 (between 1.9 and 4.3%) and 3 (between 4.8 and 7.3%) fronds to the total biomass of these classes was low at both sites. However, 50.6% of the total Class 5 biomass at Rustico was contributed by mature fronds.

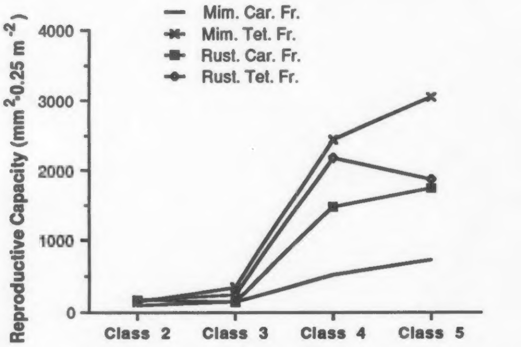

FIG. 6. Reproductive capacity of Classes 2–5 (see Fig. 3 for abbreviations).

Sorus Density per Frond

Carposporangial and tetrasporangial sori occurred on Class 2–5 fronds; Class 1 fronds were never observed to be reproductive. The mean density of sori per frond increased markedly with each class (Table 2). The mean density of tetrasporangial sori per frond per class was always higher than that for carposporangial sori. There was little seasonal difference at either site in mean density of sori per frond for Classes 2 and 3, which was in contrast with that of Classes 4 and 5. The seasonal pattern of mean carposporangial sorus density per frond was unimodal in both locations; minimal densities occurred in July (Fig. 3). The seasonal pattern of tetrasporangial sorus density per frond was bimodal at both sites, with peaks in June and November. The mean density of carposporangial and tetrasporangial sori per frond was significantly higher at Rustico than at Miminegash, carposporangia by a factor of 1.9 and tetrasporangia by a factor of 1.3 (Table 2).

Sorus Density per 0.25 m^2

The seasonal pattern in mean density of carposporangial and tetrasporangial sori per 0.25 m^2 paralleled ($r = 0.86$) that of

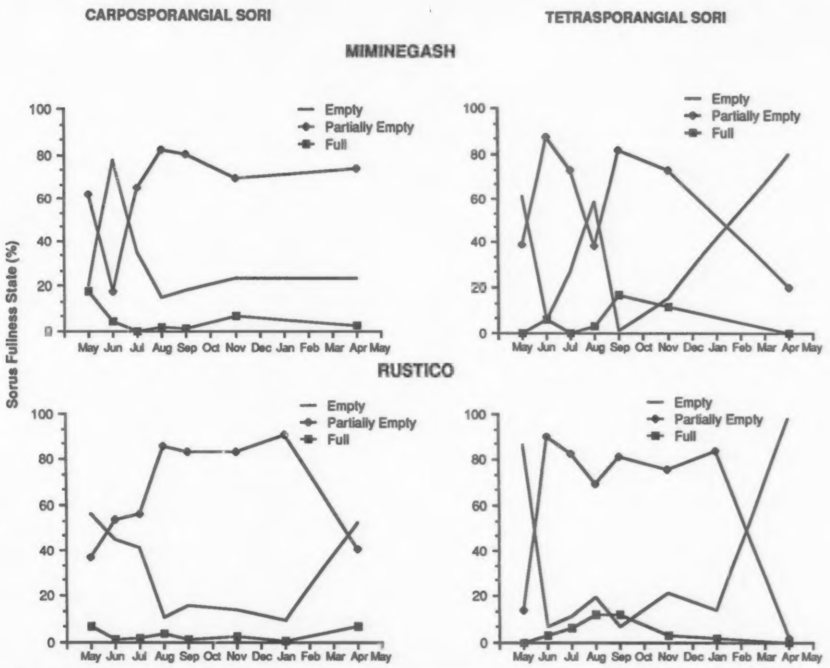

FIG. 7. Fullness state of carposporangial and tetrasporangial sori from May 1985 to April 1986 at Miminegash and Rustico.

cystocarpic and tetrasporic frond biomass, which had a similar seasonal pattern to frond density (Fig. 2). The only differences were, first, that the carposporangial sorus maxima contributed by Class 4 and 5 fronds at Miminegash were of the same order in June and September, and second, that the tetrasporangial sorus maximum of these classes at Rustico was in November instead of September. The sorus density per 0.25 m^2, contributed per frond class, increased exponentially to Class 4 and then levelled off (Table 2). There were significantly greater densities of carposporangial sori per 0.25 m^2 contributed by each frond class at Rustico than at Miminegash (Table 2). Overall, there were 3.5 times more carposporangial sori per 0.25 m^2 at Rustico (3406.8) than at Miminegash (974.4). The mean density of tetrasporangial sori per 0.25 m^2 was much higher at Miminegash than at Rustico in June; however, from late summer and during winter, this density was larger in Rustico due to a higher density of Class 4 and 5 tetrasporangial fronds (Fig. 2) and a higher number of tetrasporangial sori per frond (Fig. 3). Thus, there was no significant difference between the two sites either within each class or overall (Table 2).

Sorus Area

Mean area of both carposporangial and tetrasporangial sori varied significantly with season at both Rustico and Miminegash. The pattern was similar in each frond class; hence, these data per site were combined (Fig. 4). Carposporangial sorus area peaked in June and September at both sites; it was minimal in August and late autumn/winter. The pattern in tetrasporangial sorus area was unimodal, with the largest sori occurring in June. For both types of sori, there was no relationship between sorus area and either frond size or sorus density per frond ($r = 0.15$).

Mean carposporangial sorus area for Miminegash fronds was significantly larger in all frond classes (16% larger overall) than those from Rustico fronds (Table 3). There was no significant difference in overall mean tetrasporangial sorus area between the two study sites.

Reproductive Capacity

Carposporangial reproductive capacity (Fig. 5) was bimodal at both locations; maxima in Miminegash occurred in June and September. A similar pattern was observed at Rustico, except that the spring maximum occurred earlier (May). Variations in tetrasporangial reproductive capacity for both Miminegash and Rustico followed the same seasonal pattern as for carposporangial reproductive capacity. The contribution to the overall reproductive capacity by Class 2 and 3 fronds was low (Fig. 6). With the exception of tetrasporophytes from Rustico, there was an increase in reproductive capacity by Class 5 fronds over Class 4 fronds. The reproductive capacities of Rustico's Class 2, 4, and 5 carposporangial fronds were significantly larger than those from Miminegash; thus, Rustico's overall carposporangial reproductive capacity was greater by 58% (Table 3). The reproductive capacities of Miminegash's Class 3 and 5 tetrasporangial fronds were significantly greater than those from Rustico. However, there was no significant difference in the overall tetrasporangial reproductive capacity between Miminegash and Rustico.

Fullness State of Sori

Seasonal variations in sorus fullness for each frond class at each location were similar for both carposporangial and tetrasporangial sori; therefore, data for all classes were combined

TABLE 4. Mean percentage of sorus fullness state of the different frond classes in Miminegash (M) and Rustico (R). Asterisks indicate significant ($P \leq 0.05$) differences between the two locations.

Reproductive type	Fullness state	Class 2		Class 3		Class 4		Class 5		All classes	
		M	R	M	R	M	R	M	R	M	R
Carposporic	Empty	30.2	29.0	29.6	32.6	32.1	34.9	34.9*	27.2*	31.6	31.3
	Partially empty	61.2	65.9	64.5	61.7	65.5	63.6	61.8*	70.6*	63.6	65.5
	Full	8.6*	5.1*	5.9	5.7	2.4	1.5	3.3	2.2	4.8*	3.2*
Tetrasporic	Empty	27.6*	34.6*	33.8*	40.7*	27.9	26.4	22.5*	29.8*	28.2*	30.8*
	Partially empty	63.8	58.6	60.3	57.6	65.7	67.9	73.0*	67.4*	65.5	64.5
	Full	8.6	6.8	5.9*	1.6*	6.5	5.7	4.6	2.8	6.3*	4.5*

(Fig. 7). Partially empty carposporangial sori were abundant for most months but June in Miminegash and from April to July in Rustico. Directly opposed was the seasonal pattern of empty carposporangial sorus abundance in both Miminegash and Rustico. The incidence of full carposporangial sori never attained more than 17.5% (May) in Miminegash and 6.8% (April) in Rustico. The remainder of the year, with the exception of November at Miminegash, the percentage of full carposporangial sori was low. The seasonal pattern of partially empty tetrasporangial sori showed two maxima (June and September) and two minima (spring and August) in Miminegash. The pattern was similar for Rustico fronds, although the August minimum was not as marked. The seasonal pattern for empty sori at both Miminegash and Rustico was the reverse of the partially empty pattern. The incidence of full tetrasporangial sori was low at both study sites. The seasonal pattern was bimodal at Miminegash, peaking in June and September. The pattern was unimodal at Rustico, peaking in August–September.

The fullness state of both carposporophytes and tetrasporophytes was remarkably similar between the two study sites (Table 4). For example, the overall percentage of empty carposporangial sori was about 31.5% at both locations; the percentages of partially empty carposporangial and tetrasporangial sori were not different. There were significant differences, however; the incidences of full carposporangial and tetrasporangial sori were greater at Miminegash (4.8 and 6.3%) than at Rustico (3.2 and 4.5%), and there were more empty tetrasporangial sori in Rustico (30.8%) than in Miminegash (28.2%).

Discussion

Frond density was greater in Miminegash than in Rustico due to a greater abundance of small fronds (Classes 1–3). Fishing may be the cause, as dragraking selectively removes large fronds (Pringle et al. 1981). The initiation of frond development from the holdfast may be triggered by the removal of large fronds. Taylor (1973), however, showed that removal of the large frond canopy did not promote frond increase in length.

The early summer and autumn maxima of carposporangial (Fig. 2) frond densities agree with previous observations (for reviews, see Chopin 1986; Pringle and Mathieson 1986). On the other hand, the tetrasporangial frond density maxima occurring at the same time are contrary to the observations of most authors. Generally, these maxima occur from autumn to spring. However, comparing the results of studies on reproductive occurrence in *C. crispus* is difficult because there is not always a clear indication if distinction between the isomorphic gametophytic and tetrasporophytic thalli was made only when plants were mature (as in our case), or considering both vegetative and sporangial fronds (by use of the method of Craigie and Leigh (1978), based on the fraction of carrageenan present in the individuals).

The summer minimum for mature frond densities occurring 1 mo apart at both locations suggests that the two generations respond differently to gross environmental factors. Seasonal variations in tetrasporophytic frond densities were more pronounced than that of cystocarpic ones. Similar observations have been reported for *C. crispus* from New Hampshire (Mathieson and Burns 1975) and Massachusetts (Prince and Kingsbury 1973) and for other species (Zaneveld and Barnes 1965; Abbott 1980; Hannach and Santelices 1985). Our observations appear to support the hypothesis of Hannach and Santelices (1985) of a greater sensitiveness of the tetrasporophytic generation to seasonal changes.

Reproductive frond density was higher in Rustico than in Miminegash (Table 1). As well, the ratio of the densities of carposporangial to tetrasporangial fronds in the non-dragraked bed was about 2:1 whereas it was about 1:1 in the dragraked bed. The ratio found in Rustico is typical of that found in *C. crispus* beds elsewhere (Chen et al. 1973; Wright 1981; Bhattacharya 1985). There is no apparent reason for the decrease in fruiting carposporophytes at Miminegash, particularly where in 1977 the ratio of *n* to 2*n* fronds (based on the detection of carrageenan types) was 3:1, similar to that found in Rustico and North Lake, Prince Edward Island (Craigie and Pringle 1978). As well, in 1985–86 the density of fruiting tetrasporophytes was similar between Rustico and Miminegash. Thus, either the natural environmental conditions in Miminegash do not favour the carposporangial formation process or there is a factor(s) selecting for the potential carposporangial fronds. We hypothesize that dragrakes select for these fronds.

Although frond density was significantly greater in Miminegash than in Rustico, biomass per unit area of bed was significantly higher in Rustico. Causes for this were twofold: first, there were significantly greater numbers of Class 4 and 5 carposporangial fronds in Rustico; second, the mean individual frond weights of these classes were greater in Rustico (Class 4, 0.22 vs. 0.26 g; Class 5, 0.43 vs. 0.65 g). Interestingly, tetrasporangial mean frond density and frond weight did not differ (except in Class 3) between the two locations. Given the intense harvest pressure in the Miminegash bed (Pringle and Semple 1984) and the selection by the dragrakes for larger frond classes (Pringle et al. 1981) this finding was unexpected.

Generally, the patterns of the various studied parameters differed little between Miminegash and Rustico for frond Classes 1, 2, and to a lesser extent 3, which happened to be the classes less directly affected by dragrakes. In fact, values were frequently higher for these classes in Miminegash than in Rustico. However, these fronds were small in size and contributed little to the overall reproductive capacity.

The tretrasporangial reproductive capacity was much higher at both sites than the carposporangial reproductive capacity (Table 3). The increased production of haplopid spores that would result could, in part, account for the higher gametophytic densities observed in Rustico as in several other *C. crispus* populations (Chen et al. 1973; Mathieson and Burns 1975; Craigie and Pringle 1978; Wright 1981; Bhattacharya 1985; Chopin 1985) and in those of other Gigartinaceae (Chen et al. 1974; Abbott 1980; Dyck et al. 1985; Hannach and Santelices 1985; May 1986). In Miminegash, where carposporangial and tetrasporangial bearing fronds are equally dense, the higher tetrasporangial reproductive capacity may be countered by diploidy conferring better resistance than haploidy to the stress of dragraking. Diploid rigour under stress has been noted in other benthic algal taxa (see Pringle (1986) for a partial review) and in terrestrial plants (Stansfield 1977).

The results of the study suggest rejection of the null hypothesis that *C. crispus* reproductive capacity, measured as sporangial area, is not significantly different between intensely dragraked (Miminegash) and non-dragraked (Rustico) beds. The carposporangial reproductive capacity in the non-dragraked bed was greater, by a factor of 2.4, over that in the dragraked bed, and this was in spite of the latter site having fuller and larger carposporangial sori. The percentage of full sori remained low at both sites; thus, differences at this level would not have a major impact. The greater carpospore production in Rustico was due to the following: first, frond densities were greater by a factor of 2.0 for those classes with significantly greater carposporangial reproductive capacity; second, the biomass of these fronds was greater by a factor of 2.5; and third, the carposporangial sorus densities per frond were greater by a factor of 1.8.

Of interest is the observation that tetrasporangial reproductive capacity was not significantly different between the two study sites. Except for the tetrasporangial sorus density per frond, which was significantly higher in Rustico than in Miminegash, all other studied parameters were not significantly different between the two locations. The tetrasporangial reproductive capacity at Miminegash had a high potential at the end of spring. However, dragraking decreased it dramatically for the rest of the year to a level below that of Rustico.

Obviously, it would be of prime interest to define a harvesting technique that preserves Class 4 and 5 fronds. However, the present use of dragrakes makes this proposal unrealistic. The dragraked population (Miminegash), unlike the non-dragraked population, yielded a maximum in reproductive capacity in June, the traditional opening of the season (June 10). Harvesting quickly removed the reproductive base (Fig. 2 and 5). Unfortunately, little is known about the relationship between spore production and recruit number in macroalgae. Hence, based on these reproductive data, it would be prudent to delay the present opening date of the Irish moss dragrake fishery for up to 30 d. This period is one of low natural mortality and important for growth (T. Chopin and J. D. Pringle, unpubl. data). Furthermore, carrageenans may quantitatively improve during this time (D. J. Stancioff, FMC Corp., Marine Colloids Division, Rockland, ME 04841, USA, pers. comm.).

To optimize the yield of macroalgae requires detailed knowledge of plants and responses of beds to various harvesting practices (Vadas and Wright 1986). Cousens (1985) found that *Ascophyllum nodosum*, in low-density beds, reproduces spores at a higher level and at an earlier age and smaller size than in dense beds. This response is common for terrestrial plants. However, Schiel (1985) showed the opposite results for *Sargassum sinclairii* and *Carpophyllum maschalocarpum*. The difference in reproductive capacity of the carposporophytes between Miminegash and Rustico supports Cousens' (1985) concept. However, our data on the tetrasporophytic generation yield an intermediate situation between the observations of these two authors. The perennial holdfast is a source of recruits via vegetative reproduction. Vegetative reproduction seems to be associated with long-term maintenance of space (Dixon 1965), whereas sexual reproduction promotes colonization of new spaces (Benson 1986). Obviously, in heavily harvested dragraked beds, where holdfast mortality is high (Pringle 1978), both sources of recruits are required. Periodic recruitment, combined with high survivorship, forms multiaged populations which may be less susceptible to significant losses during bad weather conditions than those of uniform age (Rosenthal et al. 1974).

Acknowledgements

The first author is grateful to the following: Dr. G. Y. Conan who arranged his stay in Canada; Department of Fisheries and Oceans, Gulf Region, for providing facilities and financial support during 1985–86; and Drs. J. E. Stewart and M. Sinclair, Department of Fisheries and Oceans, Scotia–Fundy Region, for providing space and laboratory equipment during the last three months of this study. We are grateful to the Prince Edward Island Department of Fisheries and Labour, in particular F. Herring, for providing summer help (K. Kelly, C. Gavin, D. Callaghan, and J. Gaudet). R. Johnston, PEI Area Director for Federal Fisheries, Dr. G. Hare, and Dr. L. Hanic were supportive in many ways. The latter and Dr. C. Lobban kindly reviewed the manuscript. S. Belford, D. Duggan, R. Duggan, D. Tremblay, K. Tweel, R. Curley, and D. Gamble provided technical assistance.

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Impact of Harvesting on Irish Moss (*Chondrus crispus* Stackhouse) Frond Size-Class Structure

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Irish moss (*Chondrus crispus* Stackhouse) is cropped annually by dragrakes in certain southern Gulf of St. Lawrence Marine Plant Harvesting Districts (MPHD). Mean annual yield declined between 1972 and 1979, from peak years 1966–71, through a standing crop decrease. The present study compares frond size-class structure between three dragraked districts (light, moderate, and intense harvesting pressure) and two non-dragraked districts. Fronds, sampled by hand, were classified by pattern of dichotomy (branch) number; both mean frond weight and length were determined for each district. Frond size-class frequency distributions were bimodal from the moderate and intensely dragraked districts. Densities peaked at Classes 0 (no branching) and 5 or 6 (five or six branches), mean frond dry weights ranged from 0.09 g (intensely dragraked) to 0.18 g, mean frond length was between ~7 and ~10 cm, and mean frond dichotomy number was between ~3.6 and ~5.2. Frond size-class frequency distributions were unimodal from the non-dragraked and lightly dragraked districts, peaks were at Classes 6–8, mean frond dry weight per district was 0.40 g, mean frond length was between ~8 and ~12 cm, and mean frond dichotomy number was 7.5–8.2. The hypothesis that frond size-class frequency, mean frond dry weights, and mean frond dichotomy number were similar between intensely dragraked and non-dragraked beds was rejected. It was concluded that annual yield in the former beds would be substantially higher, were the mean frond size-class of the harvest increased by even one dichotomy. Frond length per class was not significantly different between intensely dragraked and non-dragraked beds. However, fronds higher than Class 6 from the former beds were heavier than those from the latter beds. These results are discussed in relation to dragrake selection pressure.

La mousse d'Irlande (*Chondrus crispus* Stackhouse) est récoltée annuellement par des dragues à râteaux dans certains districts de récolte de plantes marines (DRPM) du sud du golfe du Saint-Laurent. Le rendement annuel moyen a baissé entre 1972 et 1979, comparé aux années record 1966–1971, à cause d'une baisse de la biomasse. La présente étude compare la structure de classes de taille de frondes entre trois districts dragués (à récolte légère, moyenne et intensive) et deux districts non dragués. Les frondes, échantillonnées à la main, ont été classifiées par patron de nombre de dichotomies (branches); les moyennes de poids et de longueur de frondes ont été déterminées pour chacun des districts. Les distributions de fréquence des classes de taille étaient bimodales dans les districts à draguage moyen et intensif. Les densités étaient à leur maximum pour les classes 0 (pas de branchage) et 5 ou 6 (cinq ou six branches), les poids secs moyens des frondes variaient de 0,09 g (draguage intensif) à 0,18 g, la longueur moyenne des frondes était entre 7 et 10 cm environ et le nombre moyen de dichotomies des frondes entre 3,6 et 5,2. Les distributions de fréquence des classes de taille étaient unimodales pour les districts non dragués et légèrement dragués avec des pics aux classes 6–8, le poids sec moyen des frondes par district était de 0,40 g, la longueur moyenne de frondes entre 8 et 12 cm environ et le nombre moyen de dichotomies de frondes entre 7,5 et 8,2. On rejeta l'hypothèse que la fréquence des classes de taille de frondes, le poids sec moyen des frondes et le nombre moyen des dichotomies de frondes se ressemblaient entre les champs dragués intensivement et les champs non dragués. On a conclut que le rendement moyen dans les champs dragués intensivement serait beaucoup plus élevé si la classe de taille moyenne de frondes n'augmentait que d'une dichotomie. La longueur de frondes par classe ne différait pas de façon significative entre les champs dragués intensivement et les champs non dragués. Cependant, les frondes de classes supérieures à 6 des champs dragués étaient beaucoup plus fournies que dans les champs non dragués. Ces résultats sont examinés par rapport à la sélection de la drague à râteau.

Received July 28, 1987
Accepted January 15, 1988
(J9370)

Reçu le 28 juillet 1987
Accepté le 15 janvier 1988

Chondrus crispus Stackhouse (Irish moss) has been cropped annually, by dragraking, in Marine Plant Harvesting District (MPHD) 1 since the mid-1950's (Fig. 1). The fishery was fully developed by the late 1960's (Pringle and Mathieson 1986) when the mean annual landing was 12 000 t (1966–71). The mean annual landing declined to 8 000 t between 1972 and 1979, when annual landings fluctuated markedly. Evidence was presented (Pringle 1981) that this interannual variance in yield was due to fluctuations in standing crop, not fishing effort.

The fishery, typical of most inshore fisheries, is overcapitalized (Pringle 1981). Pringle and Semple (1984) demonstrated that harvest intensity, per unit area of bed, is high. Pringle (1978) found 25% of the cropped fronds attached to holdfasts, which are an important source of recruitment (MacFarlane 1956; Taylor et al. 1981). Furthermore, 50% of these fronds appeared small from a yield perspective and were considered harvestably immature (Taylor 1973). Frond size structure data from the pre-dragrake era are not available (Pringle 1985); hence, the impact of the fishery on catch mean frond size and frond size frequency distribution cannot be determined directly. Furthermore, all known concentrations of fronds suitable for experimental harvesting have been dragraked. Thus, in an attempt to assess the impact of dragraking on frond size-class frequencies, a comparative study between dragraked and non-dragraked districts (MPHD's 3, 4, 8, and 9; Fig. 1) was carried out. The present study was designed to test the hypothesis that frond size frequencies and, hence, mean frond dry weight, and frond allometric characters of *C. crispus* were different between intensely dragraked and non-dragraked beds in the southern Gulf of St. Lawrence.

Methods

Irish moss is harvested by dragrakes (see Pringle and Mathieson (1986) for an outline of the technique) in MPHD's 1, 8, and 9 (Fig. 1). The beds in these respective districts have been heavily, moderately, and lightly raked (based on detailed knowledge of the beds in MPHD 1) for at least the previous 3 yr prior to this study. The crop in both MPHD's 3 and 4 is gathered as beached "stormtoss" only. Active dragraking was banned about 1971 (Scarratt 1973), shortly after it began, due to a concern about its impact on lobster. The heavily dragraked beds are a monoculture of *C. crispus* ($>80\%$ by weight (Pringle and Sharp 1980)). The remainder of the study sites consisted of at least 50% *Chondrus* by weight (R. E. Semple, unpubl. data). Samples were collected in 1978, in early June in MPHD 1, and in mid- to late June in the remaining districts. Fronds were handpicked by SCUBA-equipped personnel from a total of nine haphazardly chosen 0.25-m^2 quadrats (sample unit) located on the inner, middle, and outer regions of the most important commercial bed in each district. The fronds from all sample units from each bed were pooled (the sample), mixed, transported on ice to the Miminegash field station, and preserved by freezing. Small handfuls of fronds (haphazardly chosen) were removed from the thawed sample. Chosen fronds (the number of fronds assessed per bed is given in Fig. 2) were classified, using the number of dichotomies of the longest linear sequence of dichotomies found per frond (Class 0, no dichotomies; Class 9, nine dichotomies). Frond length was also recorded. The fronds per frond class per sample were dried using standard procedures. Individual frond class dry weight was calculated by dividing the total class weight by the number of fronds. Average frond weight per MPHD was determined by summing the total weight of all frond classes and dividing by the number of fronds. Mean frond length per class, or per MPHD, was determined by summing the respective individual frond lengths and dividing by the number of fronds measured. Means and standard deviations were determined using a descriptive statistics package (Nie et al. 1975).

The length data were tested for a normal distribution by using the Kolmogorov–Smirnov goodness-of-fit test (Hull and Nie 1981). Non-normal data (i.e. those that did not have a Z value <1.96, $P \leqslant 0.05$) were normalized with the $\log_{10}$ transfor-

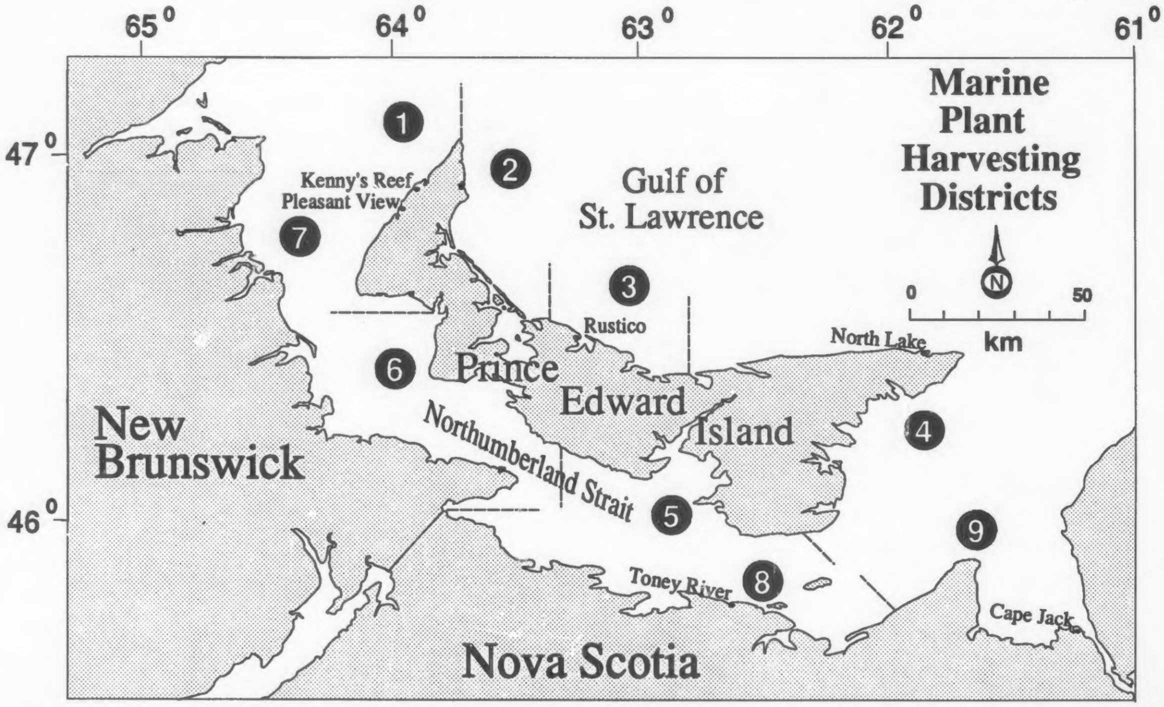

FIG. 1. Location of the study sites and the MPHD's in the southern Gulf of St. Lawrence.

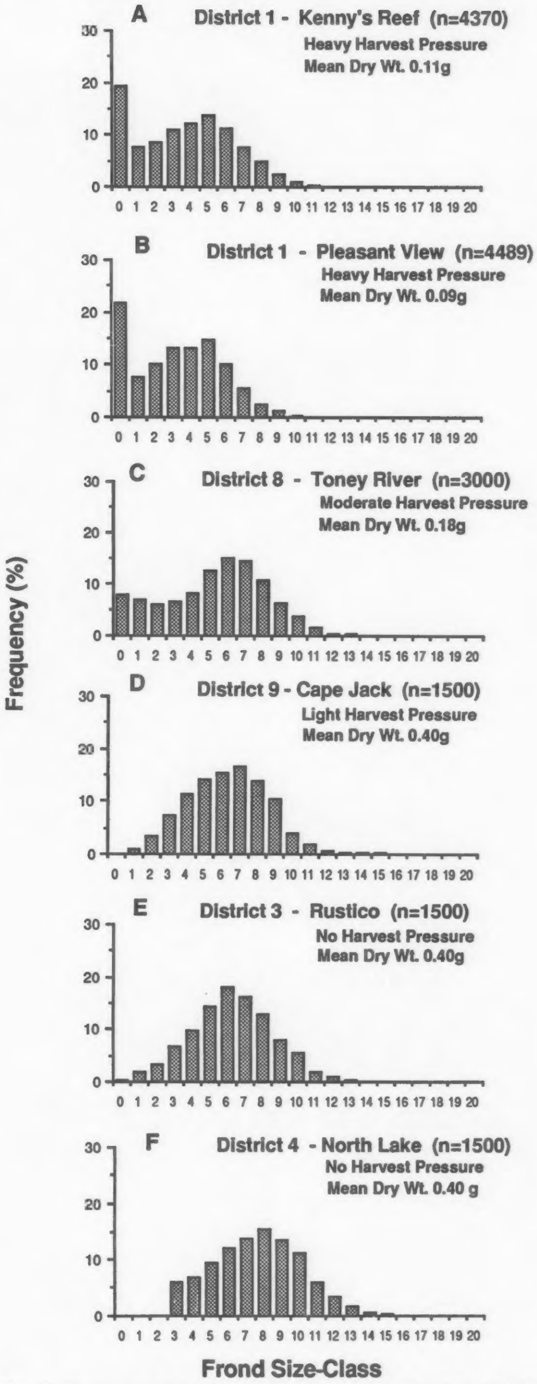

FIG. 2. Frequency of fronds per frond class for each of the MPHD's studied. Fronds were handpicked in early June 1978.

mation and tested with the one-way ANOVA and Tukey range test (Nie et al. 1975). The relationship between frond weight and size-class was assessed with a simple regression and correlation analysis (Nie et al. 1975).

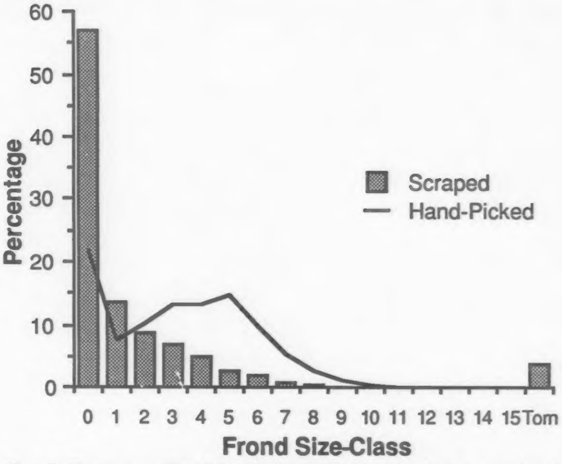

FIG. 3. Frequency (%) of fronds per frond class for both scraped and handpicked samples taken from the Pleasant View bed, MPHD 1 (heavy harvest pressure), in early June 1978.

Chondrus crispus frond length increases in direct proportion to dichotomy number to about frond size Class 9 (Pringle et al. 1987). Mean length ranged from 2.0 cm (Class 0) to 10 cm (Class 9). Samplers wearing thin gloves removed all fronds of Class 1 and greater, including only unintentionally removed Class 0 fronds. To estimate sampling error in MPHD 1, four 0.25-m^2 quadrats were haphazardly chosen in early June 1978 on a sandstone ledge in the middle of the Pleasant View bed. SCUBA-equipped personnel carefully removed all *C. crispus* holdfasts and their respective fronds from each quadrat. Each attached frond was classified as described above.

Results

Frequency Distribution

The district size-class frequencies for the handpicked samples are presented in Fig. 2. The heavy to moderate dragraked districts (MPHD's 1 and 8) have a bimodal distribution with peaks at Classes 0 and 5–6 (Fig. 2A, 2B, 2C). There was a difference in frequency of Class 0 fronds between moderately and heavily dragraked beds; these values were 8 and 22%, respectively. The absolute Class 0 frequencies would have been significantly higher given the results of the scraped sample from MPHD 1 (Fig. 3). When all Class O fronds are included, the overall frond frequency pattern changes, with Class 0 fronds being the most abundant (compare Fig. 2A with Fig. 3). The incidence of these fronds in the scraped sample was greater than the handpicked by a factor of ~2.5 (Fig. 3). The incidence of Class 12 fronds or greater was not evident in 1978 in the heavily dragraked district (MPHD 1) (Fig. 2 and 3). However, Class 13 and 15 fronds were present in the moderate and lightly dragraked districts, respectively.

The non-dragraked and lightly dragraked districts yielded a unimodal frond size–frequency distribution (Fig. 2D, 2E, 2F). The frond classes with the highest densities per district were 6 (MPHD 3), 7 (MPHD 9), and 8 (MPHD 4). Class 0 fronds were rare in MPHD 3 and absent from the samples in MPHD's 4 and 9. Surprisingly, Classes 1 and 2 were also absent from the sample in MPHD 4. There is little doubt these classes were present in the beds and included in the sample. Their densities

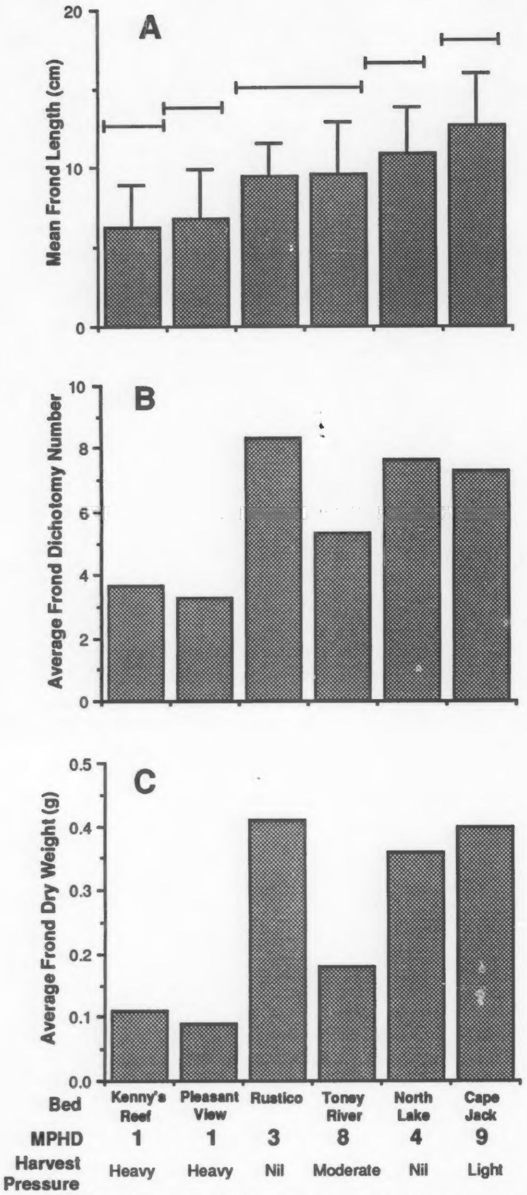

FIG. 4. (A) Mean frond length, (B) average frond dichotomy number, and (C) average frond dry weight for all fronds assessed from each of the six beds studied. The vertical lines in Fig. 4A are ±1 standard deviation; values under a common horizontal line are not significantly different ($P = 0.05$).

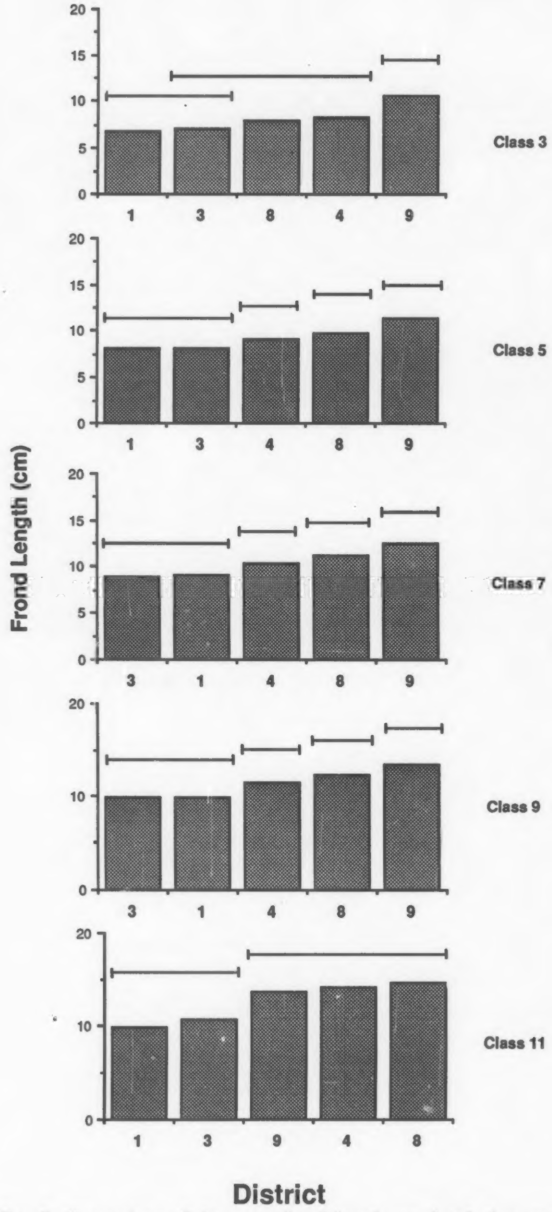

FIG. 5. Comparison of the mean frond length per frond class per MPHD. Means under a common horizontal bar are not significantly different ($P = 0.05$). Harvest pressure per MPHD: 1, heavy; 3 and 4, nil; 8; moderate; 9, light.

may have been so low that they were unnoticed and precluded from the subsample. The method was sufficiently sensitive, however, to detect all frond size-classes in MPHD 3, a non-dragraked district. Unlike the heavily dragraked district, the non-dragraked districts did have fronds in Classes 13–15.

Frond Characteristics

Interestingly, mean frond lengths were similar between a non-dragraked (MPHD 3) and the moderately dragraked (MPHD 8) districts (Fig. 4A). As well, fronds from the lightly dragraked district (MPHD 9) were significantly ($P \leq 0.05$) longer than those from all other districts. However, these long fronds did not have the greatest mean frond dichotomy number nor the heaviest mean frond dry weight (Fig. 4B and 4C). When compared with the mean frond lengths per district (Fig. 4A), their respective mean dichotomy numbers (Fig. 4B), and mean weights (Fig. 4C), fronds from MPHD's 3 and 9 appear anomalous. The short fronds from the former district were both more

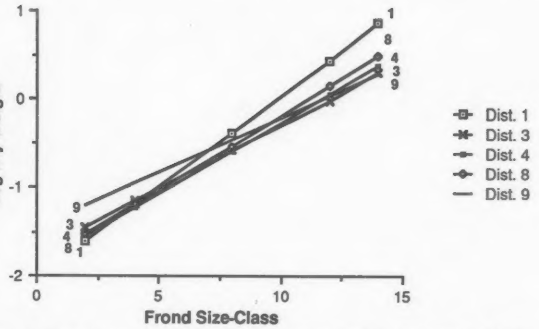

FIG. 6. Frond dry weight/frond class relationship for each MPHD. Harvest pressure per MPHD: 1, heavy; 3 and 4, nil; 8, moderate; 9, light.

heavily branched and heavier in weight than the long fronds from the latter district.

The length for certain frond size-classes from each geographic area is given in Fig. 5; an interesting pattern emerges. Fronds in Classes 3–9 from MPHD 9 (lightly dragraked) were significantly ($P \leq 0.05$) longer than fronds from all other geographic areas. By contrast, the shortest fronds ($P \leq 0.05$) in Classes 3–11 were from MPHD's 1 (heavily dragraked) and 3 (non-dragraked), and their lengths were similar. In fact, MPHD 9 Class 3 fronds were nearly as long as Class 11 fronds from MPHD's 1 and 3. The pattern of frond length in relation to branching was different again for fronds from MPHD's 4 (non-dragraked) and 8 (moderately dragraked). Fronds from these districts nearly doubled in length from Class 3 to Class 11 whereas fronds from MPHD 9 only increased by one third. There was no significant ($P = 0.05$) difference in length between the Class 11 fronds from these three districts.

The relationship between frond dichotomy number and dry weight ($\log_{10}$) for the entire data set was direct and exponential (Fig. 6). However, there was a differential in the dichotomy number/weight relationship between districts. For example, the districts that had the lightest, small size-class fronds (MPHD's 1 and 8) also had the heaviest, large size-class fronds.

Discussion

One long-term objective of our program is to optimize the yield of commercial Irish moss beds in the southern Gulf of St. Lawrence. Commercial yield is dependent on the size structure of the preharvested bed and frond size selection of the harvesting tool. Hence, evidence has been presented which permits acceptance of the hypothesis that frond size frequency and mean frond length are different in both intensely dragraked and non-dragraked beds. The mean frond weight in non-dragraked or lightly dragraked beds is greater by a factor of 4 compared with that in the intensely dragraked beds (Fig. 4C). It was not unexpected that dichotomy number yielded a similar pattern (Fig. 4B), given the relationship between frond weight and frond dichotomy number (Fig. 6). The reduced mean frond weight following intense harvesting is due to the marked increase in frequency of the small frond classes, notably Classes 0 and 1 (Fig. 2A, 2B, 2C, 3). Given that bias may have been introduced, first by the subsampling method and second by analyzing fewer fronds in the non-dragraked districts, we calculated means per district after eliminating the Class 0 fronds. Mean frond weight and dichotomy number were greater in the non-dragraked beds, compared with the intensely dragraked beds, by factors of 2.9 and 1.7, respectively.

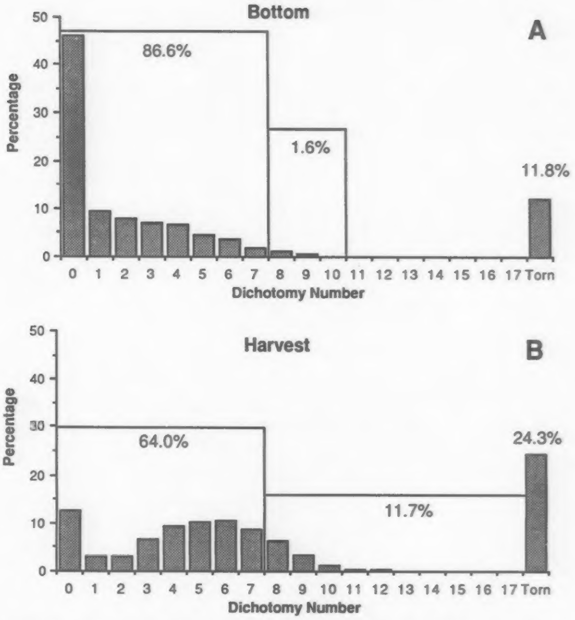

FIG. 7. Frond class frequency (%) for (A) scraped samples from the Pleasant View bed (MPHD 1) in June 1979 and (B) the harvest of a single dragraker in MPHD 1 (heavy harvest pressure) in 1979.

Annual yields have declined markedly from the period 1966–71. Since this period, there has been intense harvest pressure (Pringle and Semple 1984). Pringle (1981) showed that the annual overall commercial yield in MPHD 1 was more a function of standing crop than of harvest effort. Standing crop is a function of both frond density and mean frond biomass. Standing crop and commercial yield in the heavily harvested beds should increase if the mean frond biomass can be increased; the need appears real. For example, during the 1979 season, a season of high commercial yield compared with the previous 2 yr, the mean frond size and dichotomy number in the harvest was 0.149 g (dry weight) and ~5.5, respectively, in MPHD 1 (Pringle et al. 1987), considerably less than the means observed in unharvested beds (Fig. 4B, 4C).

One solution to enhancing the annual commercial yield in MPHD 1 is to increase the mean frond size-class in the beds. Irish moss frond dry weight increases exponentially with frond class beyond four dichotomies ($y = -1.7852 + 0.1605x$, where y is the natural log of the frond class dry weight). Were the mean frond dichotomy number in the harvest increased to 6, the annual yield would increase by 25%.

The Irish moss handrake used in the Gulf of Maine selects for the larger frond classes over the smaller frond classes (MacFarlane 1956; Sharp 1987). Data presented in Fig. 7A and 7B demonstrate the same characteristic for the dragrake employed in MPHD 1. A scraped (hand scraper) benthic sample was removed from the Pleasant View bed in early (preseason) June 1979. Frond frequency is given in Fig. 7A. Frond frequency of the 1979 dragrake harvest is given in Fig. 7B. Although 1.6% of the fronds in the bed were of Class 8 and higher, 11.7% of the fronds in the harvest were of Class 8 and higher. The latter represented 43% of the harvest weight (Pringle et al. 1987).

It appears that the solution for achieving an increased yield would not be difficult. Both frond density and biomass peak in late June–July (J. D. Pringle, unpubl. data). The period of large natural mortality occurs in the fall (J. D. Pringle, unpubl. data). Taylor (1973) demonstrated that between June and August, growth (measured as increase in frond length) of a wide variety of Irish moss frond classes in MPHD 1 was density independent. The present harvest season opening of June 11 occurs during the peak period of biomass increase. Pringle and Semple (1980) and G. J. Sharp (unpubl. data, communicated to J.D.P.) have shown that frond dichotomy number increases by between 0.5 and $1 \cdot mo^{-1}$ during this period. Consequently, were the season opening delayed only to July 1, it would permit a significant enhancement of annual yield. Another strategy that might be employed is to allow beds to lie fallow; however, experimental studies are required to determine first, if this is a reasonable option, and second, the optimum fallow period.

Given that dragraking has been intense over a period of generations in MPHD 1, one could hypothesize a change in gene frequency of the intensely harvested population. A change in those frond characteristics which would make the plant less vulnerable to the rake would not be unexpected.

Evidence of genetic change in northwestern Atlantic populations has been previously demonstrated. Chen and Taylor (1980a) described two frond morphotypes, a narrow thick form from the southeastern Gulf of St. Lawrence and a broad thin form from the northern Bay of Fundy. Laboratory experiments provided good evidence that these were indeed genecotypes and possibly distinct biological species (Chen and Taylor 1980b).

The two morphological characteristics measured in the present study were branching and length, factors that could be implicated in selection by dragrakes. For example, one might hypothesize that a shorter, less-branched frond might be less vulnerable to dragrakes. Of interest is the observation that for all classes tested (Classes 3, 5, 7, 9, and 11), fronds from MPHD 1 were significantly shorter than those from all other districts but the non-dragraked MPHD 3 (Fig. 5). Thus, either the MPHD 1 fronds from the pre-dragraked era were significantly longer, and selection has reduced frond length to that of MPHD 3, or selection in frond length has not occurred. Support for the latter hypothesis is derived from the fact that frond class lengths from the moderately dragraked bed in MPHD 8 are significantly longer than those from either of the non-dragraked districts (Fig. 5). Marine plants in general (see Mathieson et al. (1981) for a review) and *C. crispus* in particular (Mathieson and Prince 1973) are thought to have considerable phenotypic plasticity. Definitive experiments have yet to be reported, however, for *C. crispus*. Thus, it is premature to conclude a genetic difference between these districts.

The relationship between individual frond class weights and geographic area is of interest (Fig. 6). For fronds below Class 5, with the exception of those fronds from MPHD 9, there was little difference between districts in frond dry weight. It should be noted, however, that the fronds were lightest from the heavily dragraked district (MPHD 1). The converse was true, however, for fronds higher than Class 5. Given that these fronds were not significantly longer (Fig. 4A), then they must be thicker per dichotomy class. There are three scenarios that could account for this phenomenon: first, that it is due to sampling error (unfortunately, the frond weight data were collected in a fashion that prevented the employment of confidence limits); second, that MPHD 1 fronds exhibit a phenotypic-based range in frond thickness and the selective removal, by dragrakes, of the thin fronds the previous harvesting season resulted in a heavier frond class mean weight; and third, that the large frond classes in MPHD 1 are indeed thicker than those in the other districts and that the difference is genecotypically based. Were this the case, some feature(s) in the environment has exerted a selection pressure; this could have been the intense dragrake pressure.

To answer these questions of selection, experimental studies are required.

Acknowledgements

D. Jones and A. Wedge provided support at the Miminegash field station, C. Murphy and P. Hanic provided laboratory technical assistance, D. McKenna and P. LeBlanc provided field technical assistance, Dr. R. Misra provided statistical advice, and administrative support was provided by Dr. M. Sinclair. The manuscript was improved by a critical review by G. J. Sharp and two anonymous reviewers.

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Production of *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker (Ephemeroptera) in Dauphin Lake, Manitoba, with a Note on Weight Loss due to Preservatives

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Annual production and biomass of *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker were estimated from samples taken from May through September of 1982 and 1983 in Dauphin Lake, Manitoba. The size–frequency estimates (±2 SE) of production for *H. limbata* were 12.6 ± 2.68 g/m² (wet weight) in 1982 and 10.1 ± 2.10 g/m² in 1983. Instantaneous growth production estimates were 9.51 and 9.76 g/m² (1982) and 9.49 and 8.55 g/m² (1983) based on life history interpretations of four versus seven cohorts, respectively. Elucidation of complex life histories involving overlapping cohorts may not be necessary in order to make accurate production estimates for similar semivoltine populations. Annual $P/\bar{B}$ ratios for *H. limbata* ranged from 1.68 to 2.38. Production estimates for *E. simulans* in 1983 were 9.02 ± 3.10 and 9.90 g/m², using the size–frequency and instantaneous growth methods, respectively. *Hexagenia limbata* weight loss due to preservation in 10% formalin followed by 75% ethanol resulted in a production underestimate of 25%. Length changes of *H. limbata* in the same preservatives were not significant ($p > 0.05$). *Hexagenia limbata* was found at all stations having a silt/clay component. *Ephemera simulans* was found only on a matrix substrate of clay, silt, sand, and gravel.

On a déterminé la production annuelle et la biomasse de *Hexagenia limbata* (Serville) et de *Ephemera simulans* Walker à partir d'échantillons recueillis de mai à septembre 1982 et 1983 dans le lac Dauphin (Manitoba). Les estimations de la production selon la fréquence de tailles (±2 ET) chez *H. limbata* se situaient à 12,6 ± 2,68 g/m² (poids humide) et 10,1 ± 2,10 g/m² en 1982 et 1983 respectivement. D'après une interprétation du cycle vital de 4 et 7 cohortes, la production en terme du taux de croissance instantanée a été fixée à 9,51 et 9,76 g/m² (1982) et 9,49 et 8,55 g/m² (1983) respectivement. L'explication de cycles vitaux complexes comprenant des cohortes chevauchantes peut ne pas être nécessaire afin d'effectuer des estimations précises de la production dans le cas de populations semivoltines semblables. Les rapports annuels $P/\bar{B}$ chez *H. limbata* ont varié de 1,68 à 2,38. En 1983, les estimations de la production chez *E. simulans* s'élevaient à 9,02 ± 3,10 g/m² et 9,90 g/m², basées respectivement sur les fréquences de tailles et le taux de croissance instantanée. La perte de poids chez *H. limbata*, entraînée par la conservation dans le formol à 10 % puis dans l'éthanol à 75 %, a mené à une sous-estimation de la production de 25 %. Les variations de la longueur chez *H. limbata* dans les mêmes agents de conservation n'étaient pas significatives ($p > 0,05$). *Hexagenia limbata* était présente à toutes les stations d'échantillonnage où le substrat était composé d'argile et de limon. Par contre, *E. simulans* n'était présente que sur des substrats consolidés d'argile, de limon, de sable et de gravier.

Received December 19, 1986
Accepted January 7, 1988
(J9054)

Reçu le 19 décembre 1986
Accepté le 7 janvier 1988

In 1981 the Department of Fisheries and Oceans (Canada) started a walleye (*Stizostedion vitreum vitreum*) enhancement and rehabilitation project on Dauphin Lake, Manitoba. Techniques such as habitat rehabilitation, fishing regulation adjustments, and hatchery- and pond-reared stock enhancement developed during the pilot project could then be applied to other aquatic habitats (J. F. Flannagan, J. A. Mathias, and W. G. Franzin, Freshwater Institute, Winnipeg, Man., unpubl. rep.). The Dauphin Lake fishery is important both commercially and for sport. However, over the past 50 yr the fishery has changed from one of walleye and lake whitefish (*Coregonus clupeaformis* to primarily northern pike (*Esox lucius*) and white sucker (*Catostomus commersoni*). The walleye catch has declined from 202 169 kg, with a landed value of $68 288 in 1947–48 (Malaher 1948), to 10 200 kg worth $15 100 in 1982–83

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(V. Grande, L. Inkster, and D. Topolniski, Freshwater Institute, Winnipeg, Man., unpubl. data). One aspect of the rehabilitation project was the identification and quantification of the benthic fauna of the lake.

The burrowing mayflies *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker are dominant members of the macrobenthic community, are known to be consumed by various species of fish including walleye (Neave 1932; Hunt 1953; Britt 1962; Ryder and Kerr 1978), and, because of their large size, are potentially important fish food items in Dauphin Lake. Published estimates of *H. limbata* production range from 3.09 to 11.5 g/m^2 (wet weight) and may depend on the animals' life history and type of lake (Hudson and Swanson 1972; Horst and Marzolf 1975; Riklik and Momot 1982; Flannagan and Cobb 1984). There are no published production estimates for *E. simulans*. The primary objective of the current research was to estimate production and biomass for these two species.

Hexagenia limbata has a complicated life cycle of multiple overlapping cohorts in Dauphin Lake (Heise et al. 1987). A second objective of this study was to assess the influence of a simple (four cohorts present over 2 yr) versus a complex (seven cohorts present) interpretation of the life history of *H. limbata* on the calculation of the production estimates for this species.

A third objective was to determine the effect of length and weight changes caused by preserving fluids on *H. limbata* production. Preservatives result in various degrees of weight loss in invertebrates (Howmiller 1972; Stanford 1973; Donald and Paterson 1977; Giberson and Galloway 1985), but the effects have not been examined for *H. limbata*.

Study Area

Dauphin Lake is a relatively large (519.3 km^2) prairie lake located in southwestern Manitoba (51°15′23″N, 99°46′12″W). The lake is thoroughly mixed at all times during the ice-free period due to wind action and the lake's shallow depth (maximum 3.5 m, mean 2.1 m). There is a control structure on the outflow which restricts annual lake level fluctuations to 0.5 m. From May to October 1982 and from May to September 1983, bottom temperature varied from 2.4 to 24.8°C, dissolved oxygen from 73.6 to 140.0% saturation, pH from 7.89 to 8.91, and total suspended solids from 2 to 363 mg/L (J. Babaluk and M. Friesen, Freshwater Institute, Winnipeg, Man., pers. comm.). Water samples taken under the ice in 1982 and 1983 contained dissolved oxygen levels of 77.8–162.6% saturation.

The lake bottom was divided into three zones based on sediment particle size. Description of sediments follows the sand–silt–clay ratio nomenclature of Shepard (1954). All except one of the offshore stations were clayey silt or silty clay. Stations at river mouths along the west shore were sandy silt or silty sand, and stations along the rocky east and north shorelines were heterogeneous, with sediments ranging from silt, sand, and gravel to rocks approximately 0.5 m in diameter. The sediments at the exceptional offshore station were either a clay/silt mixture or of the heterogeneous matrix type.

Materials and Methods

Preservative Effects

Fifty-five *H. limbata* nymphs collected on 23–25 June 1982 were held individually in vials containing dechlorinated water for 4–7 d to allow evacuation of the gut. Fresh blotted wet weight was measured to the nearest 0.1 mg on a Mettler AE 160 balance. Total body length was measured to the nearest 0.25 mm using an ocular micrometer. Nymphs were placed into 10% formalin for 1 yr then reweighed and remeasured, and placed into 75% ethanol for 12 d and once again weighed and measured.

TABLE 1. Mean percent wet weight loss (±95% CL) of *Hexagenia limbata* nymphs, by sex, after preservation in 10% formalin and 10% formalin followed by 75% ethanol.

	Formalin	Formalin followed by ethanol
All sexes combined	5.5 ± 2.9	24.9 ± 2.4
Females	4.0 ± 4.5	23.6 ± 3.8
Males	7.6 ± 4.2	26.2 ± 3.4
Immatures[a]	1.9 ± 17.6	24.0 ± 13.2

[a] Too young to sex.

Sampling

Twenty-one sample stations were arranged along transects originating at the mouths of major inflowing rivers, in order to complement benthic faunal studies of these rivers (Cobb and Flannagan 1987). Offshore stations were located by compass triangulation using onshore landmarks.

Triplicate grab samples were taken randomly at each station monthly from May to October in 1982 and from May to September in 1983. A tall modified Ekman grab (Burton and Flannagan 1973) with a semiautomatic release mechanism (Burton 1974) was used on clayey silt and sand substrates. On the matrix substrate a pneumatic grab sampler (Burton et al. 1985) was used during all but the first 2 mo.

Samples were sieved in the field through 200-μm-mesh Nitex® screens, fixed and preserved in 10% formalin, and transferred to 75% ethanol in the laboratory. Samples with a high organic matter content were hand-picked under low power of a dissecting microscope. Samples with a low organic content and large particle size were floated in a sucrose solution (S.G. = 1.20 – 1.25) and sorted using a magnifying lens. The amount of time nymphs spent in each preservative varied from approximately 4 to 11 mo in formalin and 1 to 4 wk in ethanol.

Total body length of nymphs was measured from the tip of the frontal projection to the base of the caudal filaments. All measurements were made using an ocular micrometer.

Hexagenia limbata nymphs longer than approximately 9 mm were sexed using the interior angle of the eyes (Neave 1932) and the presence or absence of male genitalia. *Ephemera simulans* nymphs longer than approximately 8 mm were sexed using the latter method only.

Production Calculations

Blotted wet weight of preserved nymphs was measured to the nearest 0.1 mg on a Mettler AE 160 balance. Total length versus preserved wet weight linear regressions were calculated for *H. limbata* (ln wet weight = 2.99 ln length − 11.5, $n = 80$, $R^2 = 0.99$) and for *E. simulans* (ln wet weight = 3.13 ln length − 12.0, $n = 33$, $R^2 = 0.99$). These equations were then used to predict the weight of unweighed nymphs, based on their total body length. Mean weights used in production calculations were increased by a factor of 1.2488 (see Results section below) to correct for weight loss due to preservatives.

TABLE 2. Monthly mean density (no./m²) of *Hexagenia limbata* nymphs in each substrate zone in Dauphin Lake, Manitoba.

Date	Sandy	Offshore clay/silt	Heterogeneous matrix
May 1982	0	152.8	0
June 1982	2.8	98.6	5.2
July 1982	8.3	74.5	12.5
Aug. 1982	25.0	106.5	128.5
Sept. 1982	11.1	94.9	59.0
May 1983	0	123.8	24.3
June 1983	0	46.7	23.5
July 1983	0	70.7	10.6
Aug. 1983	0	63.8	109.0

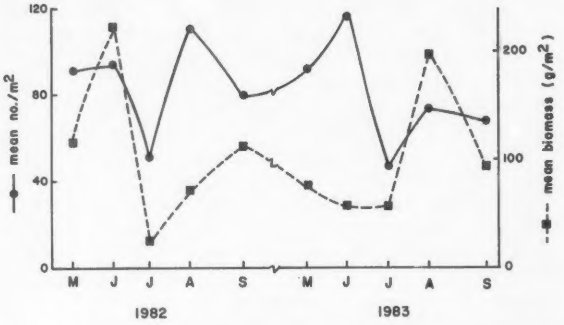

FIG. 1. Seasonal fluctuation in mean density and wet weight biomass of *Hexagenia limbata* in Dauphin Lake, Manitoba, in 1982 and 1983.

The instantaneous growth (Waters 1977) and size–frequency (Hynes and Coleman 1968; Hamilton 1969) methods of production calculation were used. For the size–frequency method the cohort production interval (CPI) correction of Benke (1979) was used and confidence intervals calculated using the method of Krueger and Martin (1980). Production estimates were calculated for *H. limbata* for 1982 and 1983. *Ephemera simulans* production was calculated for 1983 only, due to the small number of nymphs of this species collected in 1982. The instantaneous growth estimate for *E. simulans* was based on one cohort only due to the small number of nymphs collected for the older cohort.

The sand, clay/silt, and heterogeneous matrix substrates made up approximately 2.7, 95.1, and 2.2%, respectively, of the whole lake area. Biomass and production estimates of *H. limbata* were made for the silt/clay and matrix substrates only. *Ephemera simulans* estimates were made for the matrix substrate only. Whole-lake production estimates were made using the area of the entire lake.

Hexagenia limbata in Dauphin Lake has a complex life history of seven overlapping cohorts present during a 2-yr period (Heise et al. 1987). The population at first appeared to have a simple 2-yr life cycle with only four cohorts present, but by examining wing pad developmental stages in addition to length frequency and emergence data, seven cohorts were detected. Many studies of *H. limbata* populations with overlapping cohorts have found simpler life histories with fewer cohorts (Rutter and Wissing 1975; Riklik and Momot 1982; Schloesser and Hiltunen 1984). Instantaneous growth production of *H. limbata* was calculated using both a complex (seven cohorts present) and a simple (four cohorts present) division of cohorts in order to assess the impact of these two different life history interpretations on the production estimate.

Results

Preservative Effects

Length changes of *H. limbata* nymphs in formalin and formalin followed by ethanol, calculated as a percentage of fresh length, were not significant ($p > 0.05$) regardless of sex. Weight losses in nymphs held in formalin followed by ethanol, calculated as a percentage of fresh weight, were significant ($p < 0.05$) and much greater than weight losses in formalin only, averaging 24.9% overall (Table 1). There was no clear relationship between percent weight loss in formalin followed by ethanol and fresh total length of nymphs.

Substrate Preference

With the exception of one sample on one date, *H. limbata* nymphs were found in substrates having a clay/silt fraction. This included all offshore clay/silt stations and the matrix east shore. The density of nymphs in these two substrate types was usually similar (Table 2). On 12 occasions, nymphs were found at sandy west shore stations, but in 11 of these cases the substrate in the samples had some clay or silt component.

Nymphs of *E. simulans* were found only at stations along the heterogeneous matrix east and north shores. Mean densities per square metre were 63.4 (range = 0–121.5) in 1982 and 129.7 (range = 39.6–269.4) in 1983.

Biomass and Production

Hexagenia limbata

The seasonal pattern of *H. limbata* densities was similar in 1982 and 1983 (Fig. 1). Densities decreased between June and July concurrent with the major summer emergence and increased between July and August as the newly hatched nymphs appeared in the population. Numbers declined again in the fall as a second, smaller emergence took place. Densities at stations ranged from 0 to 2331/m² and standard deviations from 85 to 143% of the mean.

The mean biomass curves for the 2 yr were very different (Fig. 1), with the maximum values occurring in June in 1982 and August in 1983. In June 1982 the larger cohort was still present in the lake whereas most of the corresponding cohort had emerged by the June sampling date in 1983.

The annual production estimates for *H. limbata* calculated using the instantaneous growth method with a simple, and a complex, interpretation of cohort structure were very similar. For 1982 the complex estimate was 9.76 g/m² (Table 3) and the simple estimate was 9.51 g/m² (Table 4). In 1983 the simple estimate was 9.49 g/m² and the complex estimate was 8.55 g/m².

The size–frequency method, which does not require the identification of cohorts, produced estimates of 12.6 ± 2.68 g/m² for 1982 (Table 5) and 10.1 ± 2.10 g/m² for 1983. Both of

TABLE 3. Annual production of *Hexagenia limbata* in Dauphin Lake for 1982 using the instantaneous growth method and assuming a complex cohort structure.

Sample date	No./m^2	Mean wet weight (mg)	Biomass (mg/m^2)	Mean biomass (mg)	Inst. growth rate (*G*)	Production (mg wet weight/m^2)
			Cohort 1			
May	38.15	146.2	5 579			
				7984	0.398	3178
June	47.71	217.7	10 388			
				5292	0.092[a]	488.8
July	0.816	238.8[b]	194.9			
				97.47	0.430[c]	41.92
Aug	0	—	—			
			Cohort 2			
May	7.804	15.70	122.5			
				202.8	1.268	257.1
June	5.076	55.76	283.1			
				409.5	0.068	27.87
July	8.980	59.69	536.0			
				671.5	0.955	641.2
Aug.	5.203	155.1	807.0			
				889.1	0.415	368.7
Sept.	4.135	234.8	971.1			
			Cohort 3			
May	45.96	1.402	64.43			
				265.0	2.077	550.2
June	41.62	11.18	465.5			
				492.9	0.214	105.6
July	37.55	13.85	520.3			
				1630	1.494	2437
Aug.	44.39	61.74	2 741			
				3606	0.412	1485
Sept.	47.97	93.21	4 471			
			Cohort 4			
July	4.082	0.319	1.301			
				9.325	2.477	23.10
Aug.	4.569	3.797	17.35			
				78.14	1.710	133.6
Sept.	6.617	21.00	138.9			
			Cohort 5			
Aug.	30.68	0.335	10.28			
				18.12	1.281	23.22
Sept.	21.50	1.207	25.95			
					Total (cohorts 1–5) =	9761

[a] Calculated using males only.
[b] Extrapolated from *G* for June–July and June mean weights.
[c] Based on assumed growth to maximum observed weight.

these estimates are higher than the corresponding instantaneous growth estimates for each year.

Calculation of production using the size–frequency method with separate sexes, using a "times loss factor" (Hamilton 1969) of 6 for males and 7 for females, resulted in estimates of 11.0 g/m^2 for 1982 and 8.34 g/m^2 for 1983. Both of these estimates are lower than the corresponding size–frequency estimate using the sexes combined.

The mean production estimates from all four methods for 1982 and 1983 were 10.72 and 9.12 g/m^2, respectively. These estimates became 10.43 and 8.87 g/m^2 for 1982 and 1983, respectively, when the sandy shoreline substrate, which was not inhabited by *H. limbata*, was included in the calculation of area. *Hexagenia limbata* production over the entire lake was 5416 metric tonnes (t) in 1982 and 4606 t in 1983.

TABLE 4. Annual production of *Hexagenia limbata* in Dauphin Lake for 1982 using the instantaneous growth method and assuming a simple cohort structure.

Sample date	No./m^2	Mean wet weight (mg)	Biomass (mg/m^2)	Mean biomass (mg)	Inst. growth rate (*G*)	Production (mg wet weight/m^2)
			Cohort 1			
May	38.15	146.2	5 579			
				8014	0.383	3067
June	48.73	214.4	10 449			
				5323	0.116[a]	619.0
July	0.816	240.9[b]	196.7			
				98.32	0.421[c]	41.44
Aug.	0	—	—			
			Cohort 2			
May	53.76	3.477	186.9			
				437.6	1.466	641.7
June	45.68	15.07	688.3			
				872.3	0.410	357.6
July	46.53	22.70	1056			
				2756	1.105	3044
Aug.	65.04	68.51	4456			
				5016	0.341	1709
Sept.	57.90	96.31	5576			
			Cohort 3			
July	4.082	0.319	1.301			
				15.02	0.674	10.12
Aug.	45.96	0.625	28.74			
				29.92	0.801	23.96
Sept.	22.33	1.393	31.10			
					Total (cohorts 1–3) =	9514

[a]Calculated using males only.
[b]Extrapolated from *G* for June–July and June mean weights.
[c]Based on assumed growth to maximum observed weight.

The annual $P/\bar{B}$ ratios and their corresponding production estimates are listed in Table 6. The $P/\bar{B}$ values ranged from 1.7 to 2.4. Cohort $P/\bar{B}$ ratios ranged from 0.832 to 3.58 (complex cohort structure) and from 0.832 to 2.65 (simple cohort structure) in 1982 and from 1.64 to 2.8 (complex) and from 2.06 to 7.75 (simple) in 1983. The lowest value was for a cohort in the few months prior to emergence, and the highest value was for a cohort newly hatched.

Ephemera simulans

Annual production of the one cohort of *E. simulans* in 1983, calculated using the instantaneous growth method, was 9.90 g/m^2. The size–frequency estimate for all cohorts present during 1983 was 9.02 ± 3.10 g/m^2. The mean of the two estimates was 9.46 g/m^2, or 110 t, in 1983.

The annual $P/\bar{B}$ ratios for *E. simulans*, calculated using the instantaneous growth and size–frequency methods, were 2.94 and 2.15, respectively.

Production estimates for both species combined was possible for 1983 only. Total burrowing mayfly production in the rocky matrix habitat was 18.58 g/m^2. Whole-lake production was 9.08 g/m^2 (90.8 kg/ha), or 4716.7 t.

Discussion

Preservative Effects

The weight loss in preservative and subsequent underestimate in production of 25% for *H. limbata* is a large source of bias in the production estimate, one which is not addressed by the confidence limit calculations of Krueger and Martin (1980). Many researchers either do not comment on weight loss effects (e.g. Horst and Marzolf 1975; Flannagan and Cobb 1984), or they rely on shrinkage data for very dissimilar taxa (e.g. Riklik and Momot 1982).

In other studies, preservative effects were related to taxa, type of preservative, and length of time in the preservative (Howmiller 1972; Stanford 1973; Donald and Paterson 1977). All production studies should take this bias into account. The best way to do this is to use fresh weights. A second technique is the application of a correction factor to the preserved weights, as was done in this study. Reducing such systematic errors will increase the comparability of production estimates.

Production

The slightly higher production estimates for *H. limbata* using the size–frequency method compared with the instantaneous

TABLE 5. Annual production of *Hexagenia limbata* in Dauphin Lake for 1982 using the size–frequency method.

Size group (mm)	No./m²	Mean weight (mg)	Standing crop (mg/m²)	No. lost/m²	Geometric mean weight (mg) at loss	Biomass lost (mg/m²)	×7 production (g/m²)
0–5	20.80	0.544	11.31				
				6.587	1.764	11.62	0.081
5–10	14.21	5.723	81.34				
				0.371	11.92	4.419	0.031
10–15	13.84	24.84	343.8				
				−6.17	41.61	−256	−1.80
15–20	20.01	69.70	1395				
				7.708	97.80	753.8	5.277
20–25	12.30	137.2	1688				
				7.302	186.5	1362.0	9.531
25–30	5.003	253.4	1268				
				2.997	315.7	946.0	6.622
30–35	2.007	393.3	789.2				
				2.006	393.3	789.2	5.524
						Total =	25.27

$$\text{Annual production} = 25.27 \times \frac{365}{730^{a}} = 12.63 \pm 2.68^{b}$$

[a] This is the cohort production interval (CPI) of Benke (1979).

[b] Confidence interval = ±2 standard errors, calculated using the method of Krueger and Martin (1980).

TABLE 6. Summary of production (g/m²) and annual $P/\bar{B}$ ratio estimates for *Hexagenia limbata* in Dauphin Lake for 1982 and 1983.

Calculation method	1982	1983
Instantaneous growth (simple)	Prod. = 9.51	9.49
	$P/\bar{B}$ = 1.68	2.38
Instantaneous growth (complex)	Prod. = 9.76	8.55
	$P/\bar{B}$ = 1.78	2.05
Size–frequency (sexes together)	Prod. = 12.6 ± 2.68[a]	10.1 ± 2.10[a]
	$P/\bar{B}$ = 2.26	2.32
Size–frequency (sexes separate)	Prod. = 11.0	8.34
	$P/\bar{B}$ = 2.04	2.11

[a] Confidence interval = ±2 standard errors.

growth method are consistent with the findings in other studies (Hudson and Swanson 1972; Waters and Crawford 1973; Cushman et al. 1978; Riklik and Momot 1982). However, all of the production estimates within each year were within the 95% confidence interval of the size–frequency estimate.

Differences between the production estimates for 1982 and 1983 were small, ranging from 0 to 32% depending on the method of calculation. Annual fluctuations in production could result from changes in the growth rate of nymphs, caused by fluctuation in temperature and the food supply. One of the assumptions of the size–frequency method is that all individuals reach the same maximum size (Hamilton 1969), a condition which is not met in *H. limbata* due to sexual dimorphism. This is the most likely reason for the slightly lower estimate resulting from the calculation of sexes separately (Table 6).

Accurate determination of voltinism and length of the life cycle is essential to cohort based production methods (Waters 1979), so the agreement between estimates based on simple and complex cohort structure was unexpected. The differences among cohorts in the *H. limbata* population in Dauphin Lake were probably not large enough to influence the production estimate. Elucidation of complex life histories involving overlapping cohorts may not be necessary for accurate production estimates in this species.

The mean annual production estimates of 10.43 and 8.87 g/m² for 1982 and 1983, respectively, are among the highest reported for this species. Horst and Marzolf (1975) reported a value of 3.09 g/m² for a population in a Kansas reservoir, and Riklik and Momot (1982) estimated *H. limbata* production at 4.78–5.59 g/m² in Savanne Lake, Ontario. Production of *H. limbata* in Dauphin Lake is also higher than values of 1.0 and 7.07 g/m² in the north basin and narrows, respectively, of nearby Lake Winnipeg (Flannagan and Cobb 1984). However, comparison of production estimates is difficult due to differences in methodology, such as the manner in which weights are measured.

The whole-lake production estimates of 5416 t (1982) and 4606 t (1983) indicate that *H. limbata* provides a large potential food source for fish in the Lake. The high Dauphin Lake values probably result from the high proportion (95.1%) of the total lake area which is suitable habitat for *H. limbata*. The shallow depth of the lake also provides adequate oxygen concentrations to all parts of the lake at all times of the year.

The calculation of burrowing mayfly production in each substrate zone of Dauphin Lake increased the precision of the estimates and facilitate comparisons of production estimates among locations. Production studies should be based on accurate estimates of organism densities in habitat types and of the proportions of the habitats within the study area.

The low annual $P/\bar{B}$ ratios for *H. limbata* in Dauphin Lake are consistent with reports of values in the range of 2.0–2.6 for semivoltine populations (Riklik and Momot 1982; Flannagan and Cobb 1984). Higher $P/\bar{B}$ ratios of 3.48–5.38 have been reported for populations that are at least partly univoltine (Horst and Marzolf 1975). Mann (1967) and Waters (1969) predicted $P/\bar{B}$ ratios of approximately 2 for semivoltine and 5 for univoltine populations.

There are few studies of non-ephemerid mayfly production in lentic waters. Annual production of *Brachycercus* sp. in a pond (Benson et al. 1980) was slightly higher, at 1.9 g/m^2 (dry weight), than in this study. The many studies of mayfly production in lotic waters have found values higher (Waters and Crawford 1973; Hall et al. 1980; MacFarlane and Waters 1982; Krueger and Waters 1983), lower (MacFarlane and Waters 1982; Rodgers 1982; Krueger and Waters 1983; Benke et al. 1984), and approximately the same (Waters 1966; Giberson and Galloway 1985) as those in Dauphin lake.

The production estimates reported here are the first for *E. simulans*, despite the wide North American distribution of this species (Edmunds et al. 1976). The two methods of calculation produced similar results despite the inclusion of only one cohort in the instantaneous growth calculation.

The question of whether the cohort of large individuals present in very low numbers in the spring of 1983 was simply a poor year class, or represented an alternation of weak and strong year classes, is an important one. If the low numbers are "normal," then the calculated production estimates are representative of most years. However, if *E. simulans* frequently exhibits two equally strong cohorts, as suggested by the strongly bimodal distribution of nymphs in August 1983 (Heise et al. 1987), then the production estimates calculated here should be doubled to represent the "normal" situation in Dauphin Lake. This would result in an estimate of 28.04 g/m^2 (both species combined). Either way, the combined production of *E. simulans* and *H. limbata* in the matrix east shore is very high. The rocky shore habitat in lakes may be analogous to the highly productive "snag" habitat of subtropical blackwater rivers (Benke et al. 1984). Difficulty in sampling this habitat type may be responsible for an underestimate of the productivity of rocky lake shorelines in the literature.

Acknowledgments

This research was part of a walleye rehabilitation project by the Department of Fisheries and Oceans, which provided financial support to the senior author in the form of a research grant. We thank Mr. J. Babaluk and Ms. M. Friesen for their assistance coordinating field crews and for making available unpublished data. Mr. W. Burton provided technical assistance with the sampling equipment. We thank all of the many summer students and technicians from the Freshwater Institute and the Department of Entomology, University of Manitoba, who helped in the field and laboratory and, in particular, S. Cantor, K. Donkersloot, S. Fraser, L. Ross, and D. Wright.

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Investment Decision Making by Fishermen

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Individual fishermen make investment decisions in an environment which is competitive and highly variable from season to season. Extensive variability means that economic survival must be a primary consideration in the investment decision process. In this paper, fishermen's investment decisions are modelled as a probabilistic dynamic programming problem in discrete time. Fishermen are assumed to make rational decisions based on income expectations and subject to survivability conditions to maximize the net worth of the fishing enterprise at the end of a finite planning horizon. The formal analysis of the investment model is presented and the model is applied to troller fishermen of the British Columbia commercial fishing fleet. The results present an accurate picture of actual investment decisions and provide valuable insights into the behavioral basis of investment decision making by fishermen. Understanding the investment decisions of fishermen has implications for planning and regulation in fisheries: insights gained into the key factors provide the basis for the development of strategic long-term policies that anticipate fishermen's behavior. The consequences will be a movement away from reactive, short-term policies which have characterized fisheries regulation to date.

Les pêcheurs sont appelés, individuellement, à prendre des décisions d'investissement dans un contexte de concurrence et de fluctuations marquées d'une saison à l'autre. Étant donné l'énorme variabilité des facteurs en cause, la survie économique doit être une composante cruciale du processus de décision. Dans ce document, les décisions d'investissement des pêcheurs sont modélisées sous forme d'un problème de programmation dynamique probabiliste en temps discret. On suppose que les pêcheurs prennent des décisions rationnelles fondées sur les revenus prévus, dans des conditions qui assurent leur survie économique, en vue de maximiser la valeur nette de l'entreprise de pêche à la fin d'une période de planification de durée déterminée. L'analyse théorique du modèle d'investissement est présentée, et le modèle est appliqué à des ligneurs de la flotte de pêche commerciale de la Colombie-Britannique. Les résultats brossent un tableau exact des décisions d'investissement réelles et jettent un éclairage sur les aspects comportementaux qui sous-tendent les décisions prises par les pêcheurs. Une meilleure compréhension des décisions d'investissement des pêcheurs facilitera la planification et la réglementation dans le domaine des pêches; la connaissance plus approfondie des facteurs essentiels en cause servira de fondement à l'élaboration de stratégies à long terme qui tiennent compte des comportements prévus des pêcheurs. On pourra ainsi éviter les politiques à court terme, élaborées en réaction aux événements, qui ont caractérisé jusqu'ici la réglementation dans le secteur des pêches.

Received April 23, 1987
Accepted January 11, 1988
(J9241)

Reçu le 23 avril 1987
Accepté le 11 janvier 1988

The most serious problem facing Canada's ocean fisheries is overcapitalization of the fishing fleet (Pearse 1982; Kirby 1982). Economic theorists have long acknowledged overcapitalization (and associated rent dissipation) as a consequence of the common property nature of commercial fishing (Gordon 1954; Smith 1969). Nevertheless, regulators' attempts to control this overcapacity have not been successful in practice. For example in 1969 the "Davis Plan" effectively froze the number of vessels in Canada's west coast fishery by licensing only those that showed a dependence on the salmon fishery. However, as Pearse (1982, p.79) stated,

> ...the plan has clearly failed in its main purpose, which was to control and reduce excessive *capacity*. Investment in fishing power continued as the value of the catch increased, and the capacity of the fleet, already excessive when the program began, doubled or perhaps trebled.

Fraser (1979) showed that programs such as licence limitations have not been totally successful because they merely react to the symptoms of the problem, e.g. increasing investment and pressure on fish stocks. In response, Wilen (1979) called for the design and development of alternative regulatory programs in which policy outcomes are predictable. He asserted the importance of modelling fisherman behavior "for predicting, understanding and designing efficient regulation programs." In the J. C. Stevenson Memorial Lecture, Hilborn (1985) called for a renewed effort at understanding the behavior of fishermen. He attributed the crisis in Canada's commercial fisheries in large part (p. 3)

> ...to poor understanding of the dynamics of fishermen, how they fish, and how they invest. I therefore argue that a major element of fisheries science should be the study of fishermen and fleet dynamics.

Until recently there has been little research into the decision making processes and behavior of fishermen. Of note is the work of Clark (1985) and Mangel and Plant (1985) who examined the behavior of fishermen under quota systems. Mangel and Clark (1983) modelled the effect of searching by fishing vessels in reducing uncertainty in the location of schools of fish.

In a similar approach, Eales (1983) modelled fishermen's decisions regarding the division of time between searching and fishing updated continuously as a function of changing expected profits. Bocksteal and Opaluch (1983) presented a discrete choice model of supply response under uncertainty and applied it to New England fishing firms making intraseasonal decisions about switching into other fisheries. Swierzbinski (1981) modelled fishermen's seasonal choices about what fishery to enter and how many fishing trips to make as a function of risk attitudes and profit expectations. Of particular interest is the paper by Thompson et al. (1973). In this study a stochastic dynamic programming formulation is used to model investment decisions by individual fishing firms. The dynamic model incorporates a condition that strictly guarantees survivability of the firm in all fishing periods. The present paper takes the approach of Thompson et al. (1973) and expands their definition of the state variable to include different capital types, capital financing possibilities, and income earning power effects from new investments. The survivability conditions are also made flexible to the level of risk a fisherman decision maker is willing to assume.

Investment potential in any single period depends on the fisherman's current financial and capital structure and expected future levels of net operating income. Moreover, since income may vary appreciably from season to season, new investments may then place the solvency of the fishing enterprise at considerable risk. In this paper, limitations on investment due to high income variability are incorporated into an investment decision model that makes investment contingent on the risk of survival in the fishing business to the end of a finite planning period. A discrete time probabilistic dynamic programming formulation is developed to model the investment decisions. Investment policies are determined at each year with the objective of maximizing the expected economic net worth of the enterprise at the end of the planning period. Actual investments by fishermen are estimated by employing the derived investment policies in a simulation of the stochastic system. The performance of the investment model in anticipating the extent and type of new investments over time is measured by comparing the model-generated results with actual data for a major segment of the British Columbia commercial fishing fleet — salmon trollers. The salmon fishery is by far the most important fishery resource in both quantity and value on the Pacific coast (Pearse 1982, p. 9). Trollers constitute a significant part of the aforementioned fleet.

The contribution of this research lies in the development, analysis, and application of an investment decision making model for fishermen. The model permits the analysis and evaluation of longer-term policies which incorporate and anticipate the behavior of fishermen. Better understanding of this behavior represents a departure from "reactive" and short-term regulation strategies which have characterized fisheries policies to date.

Methods

The development of the formal interseasonal investment model begins with the presentation of a dynamic decision model without survivability restrictions. The model is then revised to include constraints on investment due to survivability considerations.

Formal Model

Define the decision variables, $s_t^i \geq 0$ to denote a new investment measured in constant (deflated) dollars at annual period $t \in \{0,1,\ldots,T-1\}$, in capital of type $i \in S$ (e.g. vessels, licences, gear) from the set of investment classifications S with $|S|$ (the number of investment classes) finite. The sum $s_t = \Sigma_{i \in S} s_t^i$ represents the total new investment at time t. The initial period of the investment planning horizon is $t = 0$, and $t = T \in I^+$ is the final period.

The net worth (or owner's equity) of the fishing enterprise in real terms (i.e. discounted market values) at the end of annual period t, NW_t, is a measure of the economic value of the operation. Individual fishermen in a competitive environment seek to have higher net worth, *ceteris paribus* (Smith 1975). Net worth also indicates solvency of the operation ($NW_t > 0$). Maintaining survivability and improving economic value under highly variable conditions make maximizing net worth a reasonable criterion for investment decision making by fishermen. NW_t is defined as the difference between assets and liabilities on both current and long-term accounts of the fishing enterprise at time t. It can be expressed in terms of its components as follows:

$$(1) \quad NW_t = NW_{t-1} + NI_t - (I_t + RP_t) - TR[NI_t - D_t - I_t + r(CA_{t-1} - CL_{t-1})] + r(CA_{t-1} - CL_{t-1}).$$

In this recursive definition, NW_t is last period's net worth, NW_{t-1}, plus the net operating income (gross income from fishing less operating costs) earned in the current year, NI_t, less debt payments owing for interest, I_t, and principal, RP_t, less taxes payable, $TR[NI_t - D_t - I_t + r(CA_{t-1} - CL_{t-1})]$, plus interest (earned or expensed) on the cash carryover from the previous year (current assets, CA_{t-1}, less current liabilities, CL_{t-1}), and D_t is tax amortization (depreciation), r is the annual real interest rate on the cash account (cash balances are assumed to be invested in, or financed by, short-term instruments at the same rate of interest), and TR the annual income tax rate. All cash values are measured in constant (deflated) dollars.

The seasonal net operating income, NI_t, is the key probabilistic component in fishermen's investment decisions. It is assumed that new investments s_t^i are made to improve or maintain the earning potential of the fishing operation and thereby increase the operation's economic value. Let NI_t be the net operating income earned per fisherman during the annual period (season) t as observed by a single fisherman decision maker. The value NI_t observed may be the fleet's average or merely the fisherman's own net operating income depending on the extent of information gathering. Assume that NI_t is the realization in period t of a random variable with probability distribution function F_{NI} which depends on historically observed net operating incomes earned by individual fishermen. Average net operating income, NI_t, may change over time as a consequence of season-to-season variations in earnings (e.g. changes in world markets) which affect every fisherman. Within a particular season, after accounting for season-to-season variations in observed averages, net operating income variation among fishermen is assumed to depend primarily on the differences in capital structure of each fishing enterprise. (While some studies such as Pálsson and Durrenberger (1982) seem to justify this assumption empirically, others, including Hilborn and Ledbetter (1985), present data which suggest that capital is not a clear income discriminating factor. The latter study partially attributes observed differences to less quantitative factors such as skill and motivation of the skipper. The established, closed entry state of the troller fishery studied in this analysis suggests that skill and motivation are not significant factors in explaining seasonal income variation among fishermen.)

Investments in type *i* capital are assumed to have a particular effect on the fisherman's gross earnings and variable costs in future periods relative to the fisherman's current average seasonal levels. Define the "investment-income effect" function, $f(s_k^i)$, as the shift in net operating income (relative to the average) due to the new investment s_k^i in period $k \in \{0,\ldots,T-1\}$. The effect on a fisherman's actual net operating income at period $k+1$, $NI_{k+1}(s_k)$ immediately following a new total investment s_k is written in terms of the seasonal average observed, NI_{k+1}:

$$(2) \quad NI_{k+1}(s_k) = [NI_{k+1} - NI_L \sum_{i \in S} f(s_k^i)s_k^i$$
$$+NI_{k+1}(0),\ k=0,1,\ldots,T-1$$

where

$$(3) \quad NI_{k+1}(0) = NI_L + [NI_{k+1} - NI_L] \sum_{i \in S} y_k^i \rho_i.$$

The shift factor, NI_L, is a real-valued constant equal to the lowest historical seasonal net operating income for a single fishing operation. The first term on the right-hand side of (2) denotes the initial adjustment in the fisherman's net operating income in period $k+1$ due to the new investment s_k through the investment-income effect function $f(s_k^i)$. The second term on the right-hand side of (2), $NI_{k+1}(0)$, denotes the net operating income earned by the fisherman when $s_k = 0$. In (3), $NI_{k+1}(0)$ is defined in terms of the random average seasonal net operating income, NI_{k+1}, and the parameters y_k^i and ρ_i. The parameter y_k^i denotes the net operating income earning power from type *i* capital (relative to the average) of a fishing operation at the end of period *k*. The value of y_k^i depends on the enterprise's capital structure at the end of period *k* relative to other fishermen in the same fishery. This parameter captures the differences among seasonal incomes of individual fishing operations by attributing earning power to vessel capital configurations. For example, vessels with greater hull capacity, gross tonnage, and more electronics and gear are assumed to have a larger net operating income earning power than other vessels with less tonnage, gear, etc., *ceteris paribus*. The parameter ρ_i is the annual discount factor on income earning power for capital of type *i*. The discount factor accounts for technological improvements, learning, and the deterioration of the real earning power of aging capital equipment. Finally, the year-to-year changes in income earning power can be written

$$(4) \quad y_{k+1}^i = y_k^i \rho_i + f(s_k^i)s_k^i.$$

From (2) and (3) above, the fisherman's revised net operating income, $NI_t(s_k)$, $t=k+1,\ldots,T$, resulting from a single new investment, s_k, is given by the recursive relationship

$$(5) \quad NI_t(s_k) = NI_L + y_t[NI_t - NI_L]$$

where

$$(6) \quad y_t = \sum_{i \in S} y_t^i = \sum_{i \in S} (y_k^i \rho_i^{t-k} + f(s_k^i)s_k^i \rho_i^{t-k-1})$$

and the parameters ρ_i and $f(\cdot)$ are chosen such that the mean value of y_t over all fishermen each season *t* is normalized, i.e. $\bar{y}_t = 1$.

In order to establish the interest, I_t, principal repayments, RP_t, and depreciation, D_t, components of (1) explicitly as a function of s_k^i, we first define the financial parameters for fishermen's investments. Depreciation for tax purposes is calculated from the annual capital cost allowance (CCA) rate, c_i, for investments of type *i*. The depreciation schedule is found by applying the rate to the remaining balance for the pool of assets in each CCA class. The annual real rate of interest for short or long-term debt instruments purchased by fishermen in any period *t* of the planning horizon is denoted by r_l, $l = CL,LTL$. The short-term interest rate on cash received or borrowed is denoted by *r*, i.e. $r = r_{CA} = r_{CL}$. The term for the financing instruments purchased in any period *t* of the planning horizon is denoted by a_l, $l = CL,LTL$.

Consider now a new investment, s_k. The depreciation schedule, $D_t(s_k)$, $t = k+1,\ldots,T$, for this investment can be written in terms of s_k^i as follows:

$$(7) \quad D_t(s_k) = D_t(0) + \sum_{i \in S} d_t^i c_i$$

with $d_k^i = 0$, $s_t^i = 0$ for $t = k+1,\ldots,T$, $D_t(0)$ is the depreciation in period *t* arising from existing capital, and

$$(8) \quad d_t^i = d_{t-1}^i (1 - c_i) + s_{t-1}^i.$$

The new investment is assumed to be financed partly by funds obtained from existing wealth (i.e. disposal of existing capital of the same type) and partly by short- and long-term debt financing. Let $\beta_i(l)$, $l = CL,LTL$ represent the remaining proportions (after disposals) of new investments in each period which are financed by debt. Thus, $\Sigma_l \beta_i(l) \leq 1$. Now, given interest rates r_l and financing terms a_l, $l = CL,LTL$, it is straightforward using annuities (uniform year end annual payments) to calculate the deterministic schedule of interest expense payments, $I_t(s_k)$, and principal repayments, $RP_t(s_k)$, from period $k+1$ out to *T* which arise from debt financing of investment s_k. Writing annual payments, $I_t + RP_t$, explicitly in terms of investments s_k^i yields

$$(9) \quad I_t(s_k) + RP_t(s_k) = (I_t(0) + RP_t(0)) + \sum_{i \in S} \sum_{l} \beta_i(l) s_k^i$$
$$\times \left(\frac{r_l}{1 - (1 + r_l)^{-a_l}} \right),$$

with the repayment portion being

$$(10) \quad RP_t(s_k) = RP_t(0) + \sum_{i \in S} \sum_{l} \beta_i(l) s_k^i \left(\frac{r_l (1 + r_l)^{t-k-1-a_l}}{1 - (1 + r_l)^{-a_l}} \right),$$
$$t = k+1,\ldots,k+a_l;\ l = CL,LTL$$

where $I_t(0)$ and $RP_t(0)$ are the total outstanding interest and principal repayment in period *t* from the existing debt of the enterprise.

From (1) we can write $NW_T(s_k)$, the net worth of the enterprise at period *T* when there is new investment at period *k* only, i.e. $s_k > 0$ and $s_t = 0$, $t = k+1,\ldots,T-1$:

$$(11) \quad NW_T(s_k) = NW_k + \sum_{j=k+1}^{T} [1 + r(1 - TR)]^{T-j}$$
$$\times \{NI_j(s_k)(1 - TR) - (I_j(s_k) + RP_j(s_k)) + TR(D_j(s_k) + I_j(s_k))\}$$
$$+ ([1 + r(1 - TR)]^{T-k} - 1)[CA_k - CL_k].$$

Using (4)–(10), the impact on terminal net worth, NW_T, can be written explicitly in terms of the new investment s_k as

$$(12)\quad NW_T(s_k)=NW_T(0)+\sum_{j=k+1}^{T}[1+r(1-TR)]^{T-j}\sum_{i\in S}s_k^i$$
$$\times\left\{f(s_k^i)\rho_i^{j-k-1}[NI_j-NI_L](1-TR)-\sum_l\beta_i(l)\frac{r_l}{1-(1+r_l)^{-a_l}}\right.$$
$$\left.+TR\left[(1-c_i)^{j-k-1}c_i+\sum_l\beta_i(l)r_l\frac{1-(1+r_l)^{j-k-1-a_l}}{1-(1+r_l)^{-a_l}}\right]\right\}.$$

The objective function of the investment problem is given by the single-valued objective of maximizing expected real net worth of the enterprise at the end of the planning horizon from each new investment at k, i.e. $E\{NW_T(s_k)\}$. Since $NW_T(0)$ is a constant independent of the decision variables, then this objective is equivalent to maximizing the expected contribution to terminal net worth by each new investment at period k:

$$(13)\quad \max_{s_k,\,k=0,1,\ldots,T-1}\sum_{k=0}^{T-1}E\{\Delta NW_T(s_k)\}.$$

Since $\Delta NW_T(s_k)=NW_T(s_k)-NW_T(0)$, then we may write

$$(14)\quad E\{\Delta NW_T(s_k)\}=\sum_{i\in S}s_k^i[f(s_k^i)v_T^i(k)$$
$$-\gamma_T^i(k)],\ k=0,1,\ldots,T-1$$

where from (12), $f(s_k^i)v_T^i(k)$ is the expected terminal benefit per unit of investment of type i, s_k^i, out to the end of the planning period with

$$(15)\quad v_T^i(k)=\sum_{j=k+1}^{T}[1+r(1-TR)]^{T-j}\rho_i^{j-k-1}$$
$$\times[E\{NI_j\}-NI_L](1-TR)$$

and $\gamma_T^i(k)$ is the deterministic unit cost out to the end of the planning period of financing the new investment s_k^i out to the end of the planning horizon with

$$(16)\quad \gamma_T^i(k)=\sum_{j=k+1}^{T}[1+r(1-TR)]^{T-j}\left\{\sum_l\beta_i(l)\frac{r_l}{1-(1+r_l)^{-a_l}}\right.$$
$$\left.\times(1-TR(1-(1+r_l)^{j-k-1-a_l}))-TR[(1-c_i)^{j-k-1}c_i]\right\}.$$

The unconstrained investment model yields solutions which are independent of the actual economic state of the fishing enterprise. Simple optimal decision rules can be computed for all periods at the beginning of the planning horizon. The characterization of the solutions depends on the form of the investment-income effect function, $f(s_k^i)$ (Lane 1986).

Survivability Risk

We now introduce the risk of survival of the enterprise over the planning horizon into the investment decision process. Risk of survivability is quantified by the condition that net worth will "most likely" exceed zero over all periods of the planning horizon. The survivability constraint is given by

$$(17)\quad \Pr\{NW_t\leqslant 0\}\leqslant p_0 \text{ for all } t$$

where p_0 is a probability value given exogenously and related to the risk nature of each fisherman. If p_0 is set to zero, then investments will not be undertaken if there is any possibility that insolvency ($NW_t\leqslant 0$) may occur. As p_0 approaches 1, then all investments which have a positive expected contribution to net worth will be undertaken.

The survival or solvency condition $NW_t>0$ with probability p_0 can be expressed in terms of a lower bound on the net operating income random variable NI_t, i.e. $NI_t>\min NI(p_0)$. Taking a p_0-risk that $NW_t\leqslant 0$ is equivalent to the risk that $NI_t\leqslant\min NI(p_0)$. Given p_0 and probability distribution function F_{NI}, the lowest level of net operating income required under (17) is determined by taking the inverse of the probability distribution function, F_{NI}, i.e. $F_{NI}^{-1}\{p_0\}$.

Let $f(s_k^i)g_{t-1}^i(k)$ be the sum of the after-tax benefits from new investments s_k^i when the minimum level of net operating income anticipated under the survivability constraint, $F_{NI}^{-1}\{p_0\}$, is realized for all periods up to t, i.e. $k+1,\ldots,t-1$. Thus, $g_{t-1}^i(k)$ is analogous to $v_{t-1}^i(k)$ of (15) with $E\{NI_j\}$ replaced by $F_{NI}^{-1}\{p_0\}$. Now, using (11) and expanding, the survivability condition at period t based on investments at period $k<t$ and assuming the lowest anticipated net operating income for all periods up to t can be written

$$(18)\quad NW_t(s_k)=NW_k+\sum_{j=k+1}^{t}[1+r(1-TR)]^{t-j}\{NI_j(0)(1-TR)$$
$$-(I_j(0)+RP_j(0))+TR(D_j(0)+I_j(0))\}$$
$$+([1+r(1-TR)]^{t-k}-1)[CA_k-CL_k]+\sum_{i\in S}s_k^i[f(s_k^i)g_{t-1}^i(k)$$
$$-\gamma_t^i(k)]+\sum_{i\in S}s_k^i f(s_k^i)\rho_i^{t-k-1}[NI_t-NI_L](1-TR)>0.$$

Expanding using (3) and collecting terms in NI_t yields

$$(19)\quad NW_k+\sum_{j=k+1}^{t}[1+r(1-TR)]^{t-j}\{(1-TR)(NI_L$$
$$+[F_{NI}^{-1}\{p_0\}-NI_L]\sum_{i\in S}y_k^i\rho_i^{j-k})-C_j\}$$
$$+([1+r(1-TR)]^{t-k}-1)[CA_k-CL_k]$$
$$+\sum_{i\in S}s_k^i[f(s_k^i)g_{t-1}^i(k)-\gamma_t^i(k)]+(NI_t-NI_L)(1-TR)$$
$$\times\{\sum_{i\in S}s_k^i f(s_k^i)\rho_i^{t-k-1}+\sum_{i\in S}y_k^i\rho_i^{j-k}\}+NI_L(1-TR)>0.$$

Solving for NI_t, the lower bound on the net operating income to ensure solvency in period t is obtained:

$$(20)\quad NI_t>\frac{1}{(1-TR)}\left(\frac{\Sigma_{i\in S}\,s_k^i[\gamma_t^i(k)-f(s_k^i)g_{t-1}^i(k)]-x_{t-1}+C_t+H_t}{\Sigma_{i\in S}\rho_i^{t-k-1}[y_k^i\rho_i+f(s_k^i)s_k^i]}\right),$$
$$t=k+1,\ldots,T$$

with $g_k^i(k)=0$, $C_t=I_t(0)+RP_t(0)-TR[D_t(0)+I_t(0)]$, $H_t=(1-TR)NI_L[\Sigma_{i\in S}\rho_i^{t-k-1}(y_k^i\rho_i+f(s_k^i)s_k^i)-1]$.

The term x_t is the net worth of the enterprise at the end of period t assuming that the lowest level of net operating income anticipated under the survival constraint (17) is realized for all periods $k+1,\ldots,t$ and assuming no investment at the end of period k and for all periods up to t:

$$(21)\quad x_t = NW_k + \sum_{j=k+1}^{t} [1+r(1-TR)]^{t-j}\{(1-TR)(NI_L + [F_{NI}^{-1}\{p_0\} - NI_L]\sum_{i\in S} y_k^i \rho_i^{j-k}) - C_j\} + ([1+r(1-TR)]^{t-k} - 1)[CA_k - CL_k].$$

The expression (20) describes the most conservative relationship between NI_t and s_k given p_0 and F_{NI}. In other words, given the endogenous risk level p_0 and historically observed incomes, the decision maker visualizes the lowest anticipated result for the net operating income occurring in all future periods in which to construct a survivable investment policy for the planning horizon.

Using the survivability constraint (17), we have that

$$(22)\quad \Pr\left\{NI_t \leq \frac{\Sigma_{i\in S} s_k^i[\gamma_t^i(k) - f(s_k^i)g_{t-1}^i(k)] - x_{t-1} + C_t + H_t}{(1-TR)\Sigma_{i\in S}(y_k^i\rho_i^{t-k} + f(s_k^i)\rho_i^{t-k-1}s_k^i)}\right\} = F_{NI}\{\cdot\} \leq p_0.$$

The above condition can be written explicitly in terms of the s_k^i by taking the inverse of the probability functions, thus

$$(23)\quad \frac{1}{(1-TR)}\left(\frac{\Sigma_{i\in S} s_k^i[\gamma_{it}^i(k) - f(s_k^i)g_{t-1}^i(k)] - x_{t-1} + C_t + H_t}{\Sigma_{i\in S}(y_k^i\rho_i^{t-k} + f(s_k^i)\rho_i^{t-k-1}s_k^i)}\right) \leq F_{NI}^{-1}\{p_0\}.$$

Clearing the denominator and simplifying, we obtain

$$(24)\quad \sum_{i\in S} s_k^i[\gamma_t^i(k) - f(s_k^i)g_t^i(k)] \leq x_t, t = k+1,\ldots,T$$

which is an alternative form of the original survivability constraint (17) assuming the worst anticipated realizations of the income random variable, i.e. $NI_t = F_{NI}^{-1}\{p_0\}$. Thus, (23) implies that if the benefits exceed the costs when the lowest anticipated level of net operating income is realized, then the investment is deemed to be survivable. Formally, s_k is described as being a "$(1-p_0)100\%$ survivable" investment if and only if (24) is true.

Under two reasonable conditions, it follows that $\gamma_t^i(k) - f(s_k^i)g_t^i(k)$ is greater than zero for all i, t, and k. The first condition requires that the longest financing term on debt instruments, a_l, be at least as long as the planning horizon, T, i.e. $a_l \geq T-k-1$. The second condition assumes that in the first year of a new investment in type i capital, the per dollar (after tax) financing cost (interest plus repayment less depreciation) exceeds the per dollar increase in after tax adjusted net operating income assuming that the worst anticipated scenario is realized, i.e.

$$(25)\quad \beta_i(l)\frac{r_l}{1-(1+r_l)^{-a_l}}(1 - TR(1-(1+r_l)^{-a_l})) - TRc_i > f(s_k^i)[F_{NI}^{-1}\{p_0\} - NI_L](1-TR), l = CL, LTL.$$

As previously stated, s_k is $(1-p_0)100\%$ survivable if and only if the survivability condition holds for all intermediate periods from $k+1$ to T. With $\gamma_k^i(k) - f(s_k^i)g_t^i(k) > 0$ for all i, t, and k, Lane (1986) showed that the survivability constraint (24) can be simplified by demonstrating that $\gamma_t^i(k) - f(s_k^i)g_t^i(k)$ does not decrease as t increases and that x_t does not increase as t increases. The survivability constraint at the terminal period of the planning horizon, $t=T$, is then a dominant restriction which guarantees $(1-p_0)100\%$ survivability at each intermediate period from $k+1$ to T, i.e. $(1-p_0)100\%$ survivability is achieved if and only if

$$(26)\quad \sum_{i\in S} s_k^i[\gamma_T^i(k) - f(s_k^i)g_T^i(k)] \leq x_T,\ k = 0,1,\ldots,T-1.$$

The dynamic programming model with survivability constraints may now be stated formally. The problem is formulated as a constrained discrete time probabilistic dynamic program (Bertsekas 1976) as follows. Let $(NW_t, y_t, d_t, rp_t, z_t, cb_t)$ be the state vector of the system at time $t, t = 0,1,\ldots,T-1$.

The state dynamics equations are as follows:

Net worth:

$$(27)\quad NW_t = NW_{t-1} + NI_L(1-TR) + \sum_{i\in S}\{y_t^i[NI_t - NI_L](1-TR) - z_t^i + TR[d_t^i c_i + z_t^i - \sum_l rp_t^i(l)]\} + cb_t - C_t$$

Income effects:

$$y_t^i = y_{t-1}^i\rho_i + s_{t-1}^i f(s_{t-1}^i)$$

Depreciation:

$$d_t^i = d_{t-1}^i(1-c_i) + s_{t-1}^i$$

Interest plus repayment:

$$z_t^i = z_{t-1}^i + s_{t-1}^i\sum_l \beta_i(l)\frac{r_l}{1-(1+r_l)^{-a_l}}$$

Repayment:

$$rp_t^i(l) = rp_{t-1}^i(l)(1+r_l) + s_{t-1}^i\beta_i(l)\frac{r_l(1+r_l)^{-a_l}}{1-(1+r_l)^{-a_l}}$$

Cash balance:

$$cb_t = r(1-TR)(CA_{t-1} - CL_{t-1}).$$

The solution to this problem is a feasible investment decision rule, π, a function of the state vector which maximizes the reward functional

$$(28)\quad J_0^{\pi}(NW_0, y_0, d_0, rp_0, z_0, cb_0) = \max E\left\{\sum_{t=0}^{T-1}\Delta NW_T(NW_t, y_t, d_t, rp_t, z_t, cb_t)\right\}$$

subject to the survivability constraint (26) and the state dynamics (27). Figure 1 presents a schematic of the dynamic investment decision process.

The solution procedure to obtain π for the dynamic program is carried out using differential dynamic programming and backward recursion see also Jacobson and Mayne 1970 for details). The recursion is written explicitly as follows for $k = 0,1,\ldots,T-1$:

$$(29)\quad J_k^{\pi}(NW_k, d_k, rp_k, z_k, cb_k) = \max_{s_k^i} E\left\{\sum_{i\in S} s_k^i\left(\sum_{j=k+1}^{T}[1+r(1-TR)]^{T-j}f(s_k^i)\rho_i^{j-k-1}[NI_j - NI_L](1-TR) - \gamma_T^i(k)\right) + J_{k+1}^{\pi}(NW_{k+1}, y_{k+1}, d_{k+1}, rp_{k+1}, z_{k+1}, cb_{k+1})\right\}$$

and $J_T^{\pi}(\cdot) = 0$. The following paragraphs describe the development of the algorithm used to determine dynamic investment decision rules.

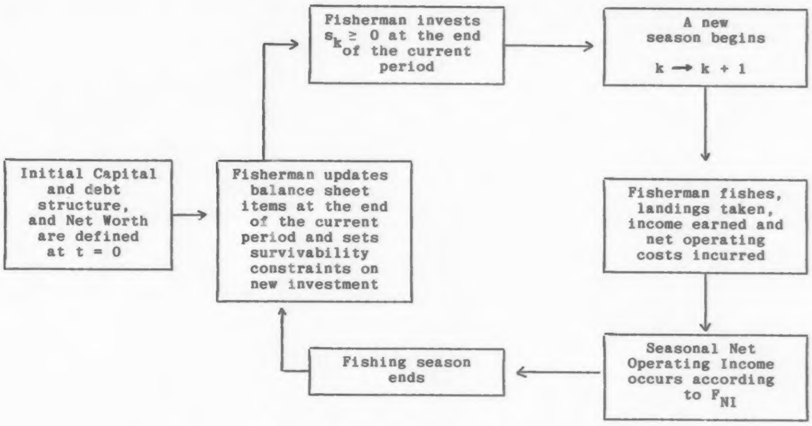
Fisherman invests $s_k \geq 0$ at the end of the current period
A new season begins
k → k + 1
Initial Capital and debt structure, and Net Worth are defined at t = 0
Fisherman updates balance sheet items at the end of the current period and sets survivability constraints on new investment
Fisherman fishes, landings taken, income earned and net operating costs incurred
Fishing season ends
Seasonal Net Operating Income occurs according to F_{NI}

FIG. 1. Interseasonal decision process.

Consider the investment-income effects model with $f(s_k^i)$ an affine function:

$$(30) \quad f(s_k^i) = q_0^i + q_1^i s_k^i \text{ for all } i.$$

Heuristic procedures are used to develop estimates for the "best" investments to be made over time. The linearization of the state dynamics equations (27) allows for the separable treatment of the investment decision subproblems at each stage of the backward recursion. The reward functional J_k^π (28) which determines the investment decision rule at each stage as a function of the state variables may be written as

$$(31) \quad J_k^\pi(\cdot) = \max_{s_k^i} \{ \sum_{i \in S} [s_k^i b_k^i + e_k^i (s_k^i)^2] + C \}, k = 0,1,\ldots,T-1$$

where

$$\begin{aligned}(32) \quad b_k^i = {} & v_T^i(k) q_0^i - \gamma_T^i(k) \\ & + D_{k+1} \{ [1 + r(1-TR)]^{T-k} [v_T^i(T-1)\, q_0^i - \gamma_T^i(T-1)] \\ & + q_0^i g_T^i(k+1) \} \\ e_k^i = {} & v_T^i(k) q_1^i + D_{k+1} \{ ([1 + r(1-TR)]^{T-k} v_T^i(T-1) \\ & + q_1^i g_T^i(k+1) \}\end{aligned}$$

and C is a constant independent of the decision variables s_k^i. Investments s_k^{i*} and factors D_{k+1} ($D_T = 0$) at each stage are determined by solving the quadratic program

$$(33) \quad Z = \max \sum_{i \in S} (s_k^i b_k^i + e_k^i (s_k^i)^2)$$

subject to the quadratic (i.e. order $(s_k^i)^2$) survivability constraint (26), and $s_k^i \geqslant 0$, $i = 1,\ldots,N_S$. The solution to this problem may be found by the method of Lagrange. For given values of the state variables and expectations about future average net operating incomes, the unique value of the Lagrange multiplier, λ, is determined by substituting the first-order necessary conditions from (33) into the nonlinear survivability constraint (26) and then solving with the constraint expressed as an equality. If the survivability constraint is binding in the optimal solution to (33) at each stage, then $\lambda > 0$ in accordance with the Kuhn–Tucker conditions. However, if the survivability constraint is not binding, then λ is zero-valued in the optimal solution. Thus, two different solutions are characterized at each stage of the problem corresponding to $\lambda = 0$ and $\lambda > 0$. Each of these possible solutions is recorded and carried forward at each stage of the backward recursion.

Now, since the values of the state variables are not known in advance at each stage of the backward recursion, we need to express λ as an explicit function of these variables in order to develop a state dependent–average income expectations policy. Using x_T (21), the right-hand side of the survivability constraint (26), and providing relevant x_T values (bounded by the problem inputs), $\lambda(x_T)$ is approximated by the first-degree (linear) interpolating polynomial

$$(34) \quad \lambda = \alpha_0 + \alpha_1 x_T.$$

Appropriate values for α_0 and α_1 are determined by minimizing the mean-square error $\sum_{j=1}^{n} (\lambda_j - \alpha_0 - \alpha_1 x_{T_j})^2$ for n pairs of values for λ and x_T. (In general, λ may be approximated by an nth-degree polynomial in x_T. The linear model (34) simplifies the recursion and permits, after lengthy algebraic manipulation, the expression of J_k^π as a simple function of x_T. For the troller data used in this analysis, the linear model (34) provides a reliable estimate of the actual function, $\lambda(x_T)$.) The value for each λ given x_T at each stage is found by the Newton–Raphson iterative procedure. Pairs of λ and x_T are generated until stable estimators of α_0 and α_1 are found. For all test problems the iterative method converged to a λ value after at most 15 iterations for each trial value x_T. Consequently, the objective function Z of the nonlinear program (33) is written in terms of the estimated parameters so that $Z = Z(x_T)$. Finally, the function $Z(x_T)$ is expanded as a Maclaurin series (i.e. a Taylor series expansion about zero) to yield

$$(35) \quad Z(x_T) = Z(0) + Z'(0) x_T + R(x_T^2)$$

where $R(x_T^2)$ is the error term arising from all terms in x_T of powers greater than or equal to 2. Assigning D_{k+1}, in (32) equal to $Z'(0)$ completes the recursion. Since Z is an increasing function of x_T, then $D_{k+1} > 0$. Once D_{k+1} is determined, then the terms b_k^i and e_k^i may be calculated at the next stage of the backward recursion from (32). If $b_k^i < 0$, then no new investments of type i are made at the end of period k.

The algorithm for computing the investment decision rules from the dynamic programming model is as follows:

(0) Set $k = T - 1$.

(1) Calculate the coefficients of the quadratic objective function, b_k^i, e_k^i, for all i given D_{k+1} (32) ($D_T=0$).

(2) Calculate D_k, from b_k^i, e_k^i, the survivability coefficients, $\gamma_T^i(k) - g_T^i(k)$, and the Maclaurin series for Z as in (35).

(3) Determine the new investment decisions as a function of the state variables.

(4) Set $k=k-1$.

(5) If $k<0$, then STOP; else GO TO Step 1.

Given investment model decision rules, the actual investment strategy proceeds by the movement of the decision process from one decision point to another over time. The actual investments in each capital type over time depend on (i) the position of the firm denoted by ($NW_t, y_t, d_t, rp_t, z_t, cb_t$) and (ii) the expectations and actual realizations of the net operating income random variable in each period over the planning horizon.

The algorithm is coded in double precision FORTRAN and run on the University of Ottawa's AMDAHL 5860 mainframe computer. Investment decision rules for each period k of the planning horizon are presented as a function of the current value x_T. A sample of investment decision rules for the model are presented in Table 1. The investment decision rule is described in terms of $x_T(k)$ (the value of x_T corresponding to a new investment in period k) and takes the form of a ratio with $x_T(k)$ appearing in the numerator and denominator. This expression assumes that the survivability constraint is binding. If the survivability constraint is not binding in period k, then the investment is given by the constant which appears after "OR" in the table.

TABLE 1. Investment models policy results. All values are in thousands of real 1971 dollars.

Period k	Periods to go	Investment type	95.0% survivable investment[a]
3	2	3	$\frac{-0.586E-04 \ -0.306E-01 \cdot X(3)}{-0.406E-02 + 0.336E-03 \cdot X(3)}$ OR 0.213E+01
2	3	2	$\frac{0.129E-02 \ -0.444E-02 \cdot X(2)}{-0.737E-03 + 0.887E-05 \cdot X(2)}$ OR 0.106E+02
2	3	3	$\frac{-0.880E-02 \ -0.568E-02 \cdot X(2)}{-0.547E-02 + 0.658E-04 \cdot X(2)}$ OR 0.378E+01
1	4	2	$\frac{-0.325E-02 \ -0.171E-02 \cdot X(1)}{-0.920E-03 + 0.336E-05 \cdot X(1)}$ OR 0.796E+01
1	4	3	$\frac{0.443E-02 \ -0.229E-02 \cdot X(1)}{-0.647E-02 + 0.237E-04 \cdot X(1)}$ OR 0.146E+00
0	5	1	$\frac{-0.261E-03 \ -0.144E-03 \cdot X(0)}{-0.281E-02 + 0.618E-07 \cdot X(0)}$ OR 0.208E+01

[a] Investment policies given in terms of $X(k)$ assume that the survivability constraint is binding. If the constraint is not binding, then the investment is independent of $X(k)$ and investment following the "OR" applies.

Actual dynamic model investments by individual fishermen using the derived investment decision rule are determined by the following sequence of events (stage k, $k=0,1,\ldots,T-1$):

(1) Update the balance sheet, NW_k, at the end of the period given actual net operating income, NI_k, capital structure, y_k^i, and cash balance, $CA_k - CL_k$.

(2) The decision maker invests s_k^i according to the investment decision rule, π, as a function of the value of $x_T(k)$.

(3) Fishing season $k+1$ begins, landings are taken, income earned, and operating costs incurred through the realization of the random variable NI_{k+1}.

(4) The fishing season ends; $k \leftarrow k+1$. Return to Step 1 if $k<T$; else STOP.

Empirical Development

The model developed above is applied to the troller segment of British Columbia's commercial fishery. Trollers, which are the largest segment (in numbers of vessels) of the commercial fleet, may catch as much as 18 tonnes of Pacific salmon in a single day. Investments made by troller fishermen are classified (for tax purposes) into four major investment types. These are classified and described as follows (Revenue Canada 1982):

Type	Investment classification	Description
1	Eligible capital	Fishing license and other government rights
2	Vessels	Boats and major component parts, e.g. engines, furniture, fixtures, hydraulics
3	Gear/electronics	Accessories to the operation, including drills, electric motor and engines, lines, ice machines, pumps, radio equipment, radar, tools over $200, welding equipment.
4	Other equipment	Equipment used as part of the fishing operation, e.g. cars, trucks, trailers, structures (buildings, wharves), chain saws, outboard motors

Actual investments in eligible capital (Table 2) usually represent a major outflow of funds and as such occur infrequently for most individual fishermen. On the other hand, gear/electronics investments require much less of an outlay of funds and are purchased more often.

TABLE 2. Troller actual investment statistics, 1973–82. All values are in real 1971 dollars.

Type i	Investment classification	Average nonzero investment	Maximum nonzero investment (year)	Average percent of investors
1	Eligible capital	14 160	49 025 (1979)	7.55
2	Vessel	13 090	209 107 (1979)	41.00
3	Gear/electronics	1 626	15 508 (1979)	43.67
4	Other equipment	2 719	25 714 (1978)	21.11

The key random component in the investment model is the average seasonal net operating income from season t, NI_t. Impacts on actual fishermen's income due to existing and new investment s^i_k are captured by y_t through the function $f(s^i_t)$ and the discounting factor ρ_i. The discount factors ρ_i and the parameters of the $f(s^i_t)$ function for all capital types i are derived from two distinct (and unrelated) databases: (1) the troller attributes database (unpublished data) and (2) the troller annual cash report database (Department of Fisheries and Oceans 1984a, 1985) for the period 1973–82. All data on individual troller operations have been disguised to protect the identity of the vessels and owners.

The 1973 (beginning of year) troller attributes database includes information about vessel value, vessel capital items, and fishing vessel licence restrictions. Among 35 separate attributes for a set of $N = 1435$ trollers, selections were made and placed into capital classifications for licence-related, vessel-related, and gear/electronics-related attributes (there are no discernable attributes related to the "other equipment" capital classification):

Type	Investment classification	Assigned attributes
1	Eligible capital	Fishing code (licence "tab" specification)
2	Vessels	Year built and rebuilt; estimated length; net and gross tonnage; estimated boat value; engine type (gas, diesel); horsepower
3	Gear/electronics	Numbers of radiophones, lorans, radar, echosounders, direction finders, autopilot, sonar
4	Other equipment	Nil

The variability among vessels of these attributes are examined for all trollers of the database. Attributes that are most often observed with low variability of occurrence among the vessels are assigned high weights. Such attributes are deemed to be more indispensible to the troll fishing activity as a result of their observed constancy over the troller fleet (e.g. length of vessel, horsepower) and consequently are less likely to explain seasonal income variation among fishermen. Conversely, low weights are assigned to attributes with the greatest variation among vessels. These attributes are not deemed to be crucial to the troll fishing activity per se by virtue of their higher variation among the fleet. Individual variations of these attributes are weighted lower (e.g. gross tonnage, boat value). This approach permits the assignment of class weights, Ω_i, to each capital type i representing troller capital attributes.

The annual cash report database provides actual annual net operating income statistics, $NI_t(s)$, for 100 trollers of the commercial salmon fishing fleet from 1973 to 1982. The distribution of NI_t, the random variable for average seasonal net operating income by individual fishermen, is based on these data assuming that realizations are calculated from small samples of actual net operating incomes among all historical values. The shift parameter, NI_L, is determined from this database item ($NI_L = -\$6098(1971)$), as is the actual average per vessel net operating income value in each year, NI_t. The normalized variable y_t, $t=1973,\ldots,1982$, is computed using these values for each of the 100 trollers as follows:

$$(36)\quad y_{tn} = \frac{NI_{tn}(s)-NI_L}{NI_t-NI_L}\ , t=1973,\ldots,1982; n=1,\ldots,100.$$

The resulting variable y_{1973} is treated as the dependent variable in a multiple linear regression against the independent variables, Ω_i, $i=1,2,3$. The regression model that results is

$$(37)\quad y_{1973n}=\phi_1\Omega_{1n}+\phi_2\Omega_{2n}+\ \phi_3\Omega_{3n}+\phi_4+\epsilon_n,\ n=1,\ldots,100$$

where the ϕ_i, $i=1,2,3,4$, are the weights assigned to relative earning potential of capital of each type i. All trollers are assumed to have the same (constant) weight for "other equipment", ϕ_4, in their capital structure prior to new investments at the end of the 1973 fishing season. The squared correlation coefficient is high ($r^2=0.9928$) and all parameters are significantly different from zero. Examination of the residuals reveals no evidence of model misspecification. The regression results establish an initial configuration description $y^i_{1973}=\hat{\phi}_i\Omega_i$, $i=1,2,3,4$, at the end of 1973 (prior to new investment taking place for the 1974 season) for all 100 trollers of the annual cash report database.

The parameters of the $f(s^i_t)$ function (30) and the ρ_i are now determined by minimizing the sum of squared errors as in the ordinary least squares approach of linear regression. In particular, given the initial capital structure y^i_{1973n} and actual investments, s^i_{t-1n} (1973-82), values for the dependent variables y^i_{tn},$t=1974,\ldots,1982$, are obtained. Now, the parameters q^i_0, q^i_1, and ρ_i, $i=1,2,3,4$, are determined which minimize

$$(38)\quad \sum_{t,n}(y_{tn}-\ \sum_{i=1}^{4}[y^i_{t-1n}\rho_i+q^i_0 s^i_{t-1n}$$

$$+q^i_1(s^i_{t-1n})^2]^2,\ t=1974,\ldots,1982;\ n=1,\ldots,100.$$

Parameter estimates (Table 3) were determined by minimizing (38) using the method of steepest descent. The values of all components of the gradient function at the final stopping point did not exceed 0.01. Investments in licenses have an initial negative effect ($\hat{q}^1_0=-0.205$) on net operating income. However, earnings effects in future years are augmented, since the discounting factor for licenses, $\hat{\rho}_1$, exceeds 1. These results may be explained by the presence of an initial learning effect due to a shift to new fishing grounds or new fishing techniques used in the capture of different species. Also, the density effects, $\hat{q}^i_1$, all have negative parameter values. This is indicative of investment capital density dependence and diminishing returns to marginal investment.

TABLE 3. Income effects parameter estimates. All initial effect and density effect parameter estimates are in terms of (transformed) net operating income effects per hundred thousand real 1971 dollars of new investment.

Type i	Investment classification	Discount factor, $\hat{\rho}^i$	Initial effect, $\hat{q}^i_0$	Density effect, $\hat{q}^i_1$
1	Eligible capital	1.156	−0.205	−0.039
2	Vessels	0.900	0.183	−0.189
3	Gear/electronics	0.795	2.680	−1.580
4	Other equipment	1.104	0.346	−3.250

Regulation requirements (e.g. on the size and replacement of vessels and gear restrictions) determine in part the investment possibilities of fishermen. Fishermen finance new investment from three major sources: (i) by increasing long-term debt (taking out a bank loan); (ii) by increasing short-term debt and/or decreasing savings (borrowing from a friend, cashing in on a term deposit, or withdrawing from a savings account); and (iii) disposing of some existing assets (selling an old vessel to build a new one). The propensity to invest depends on the ability of the fisherman to gather sufficient funds from each of these sources in order to finance the desired investment. Conversely, the set of investments which are feasible to the fisherman depend on the funds arising from these sources.

TABLE 4. Average sources of financing (percentages for each investment classification).

Type i	Investment classification	Short term	Long term	Disposals
1	Eligible capital	10	65	25
2	Vessel	15	60	25
3	Gear/electronics	15	80	5
4	Other equipment	15	80	5

Although specific data on how troller fishermen actually apportion the financing of new investments are not available, data on troller tax submissions provide insight into how fishermen finance investments of each capital type (Table 4). Proportions for debt items are estimated from year over year changes in interest payments available from annual survey data (Department of Fisheries and Oceans 1984a, 1985).

Real rates of interest and the length of the terms for financing instruments are based on the historical data for the fishing fleet of British Columbia (Department of Fisheries and Oceans 1984b; Marine Resources Branch 1979; McMullan 1981). Short-term debts are current liabilities which are assumed to be 100% payable (principal plus interest) at the end of a 1-yr term at an average real rate of interest of 2.0% (Department of Finance 1984). Long-term debts are long-term liabilities whose payments (principal plus interest) are payable in equal year-end amounts over a 7-yr term at an average real rate of interest of 4.0% per annum (Department of Finance 1984). Disposals or disinvestments in long-term assets items are assumed to be 100% refundable at existing market values. Disposals are assumed to be connected with corresponding new investment of the same type (i.e. disposals occur only when an investment takes place). Disposals are a one-time reduction to the total financing requirements for the new investment.

The length of the planning horizon for investment decisions can be surmised by considering the period over which cash flow information is knowable. There is evidence that fishermen are very myopic vis-à-vis their expectations of future income streams (Pálsson and Durrenberger 1982). Moreover, the random nature of incomes seriously restricts planning. On the other hand, investment financing plans such as the *Fisheries Loan Improvement Act* give specific information on required cash outflows (debt payments on loans) to a maximum of 10 yr in the future. Differences in the length of the planning horizon alone will result in differences in investment policies.

Results

Model Validation and Sensitivity

The investment decision model is driven by data for financial parameters and troller-specific parameters. The financial parameters include the annual income tax rate, annual depreciation rates for each capital type, annual rates and terms for short- and long-term loan financing, and the proportions for financing new investment by type among short-term and long-term loans, and disposals. The troller-specific parameters include the length of the planning period (in years), the initial capital structure of the troller operation (the current cash and net worth positions, the stream of outstanding debt payments-interest and repayment, and tax depreciation schedules, assuming no new future investments over the planning period), the initial net operating income earning power of each operation, the investment-income effects parameters, the survivability (or risk) factor, and the annual net operating income anticipated by the decision maker for the years of the investment planning period.

From these inputs, the investment decision rule (e.g. Table 1) is used to determine investments by individual trollers of the annual cash report database over the period 1973–82 for whch actual data are available. The investment results are then used in a simulation of the actual net operating incomes for each fishing season beginning in 1973. The troller's initial capital position is established (from the troller attributes data) and an initial investment is made using the dynamic investment decision rule. The seasonal net operating income for the first season following the initial (beginning of year) investment is simulated based on the revised earning power of the troller (due to the new investment) and a random disturbance related to the distribution of yearly average income. Each troller's cash and net worth position is updated and the investments for the next period are established using the policy for 1974 and the updated position of the troller. The procedure continues for each troller until the end of the planning period. For the purpose of the analysis of model sensitivity no updating of the derived investment policy takes place as time evolves, i.e. no revision is made of the net operating income anticipated for the remaining years of the planning period. Model results present average troller investment by type and average troller cash and net worth positions at each year of the planning period.

The model was also tested for a number of different investment scenarios including different planning horizon lengths, different survivability factor values, different troller income groups (selected by historical income performance), and different anticipated yearly income levels. A summary of average troller model investments for the different scenarios as compared with the "base case" results of Table 5 are found in Table 6.

The sensitivity analysis results (Table 6) show that for all scenarios, no new investment for type 4 capital (other equipment) occurs. Examination of the investment-income effects parameters reveals that other equipment investments are dominated by all other capital types. The high negative $q_1{}^4$ value and the low positive $q_0{}^4$ value relative to the corresponding values of the other capital types demonstrate this domination. In all scenarios examined, no investment takes place in the final year of any planning period. Investments in this final year do not contribute to increasing the expected net worth to the end of the planning period. In general, the additional earning power in the first year after a new investment is outweighed by the higher cost of financing the investment in its first year.

New model investment in type 1 capital (eligible capital) occurs only in the earlier years of all planning periods. This is a consequence of the high relative discount factor, ρ_1, and the more positive initial effects parameters, q_0^1 and q_1^1, resulting in no deterioration of the earning power effect for license capital.

TABLE 5. Troller average investment model results for the base case scenario with a 5-yr planning horizon, a 5% survivability factor, and yearly anticipated income equal to the actual average net operating income for trollers over the 10-yr period 1973–82. All values are in thousands of real 1971 dollars.

Year	Investment type 1	2	3	4	Net operating income	Year end net worth	Year end cash balance
1972						20.000	0.000
1973	0.976	0.000	0.000	0.000	11.356	28.563	5.270
1974	0.000	5.477	0.070	0.000	5.910	29.571	6.278
1975	0.000	8.343	3.061	0.000	3.470	27.475	4.183
1976	0.000	0.000	1.816	0.000	8.111	27.670	4.377
1977	0.000	0.000	0.000	0.000	7.628	27.027	3.734
Annual avg.	0.195	2.764	0.989	0.000	7.500	28.061	4.768

TABLE 6. Model sensitivity analysis. All values are percentage differences reported relative to the results for single variable input changes in the model reported in Table 5.

Input variable	Variable value	Annual investment 1	2	3	4	Net operating income	Net worth	Cash balance
Planning period	3 yr	−100.0	−12.5	58.5	—	−6.7	−8.7	−11.6
	5 yr[a]							
	7 yr	1653.3	−53.0	−51.1	—	20.3	10.5	−101.4
p_0	0.00	−46.8	−32.9	−21.7	—	0	2.5	14.5
	0.05[a]							
	0.10	12.1	9.6	4.1	—	0	−0.6	−3.5
Income anticipated	Pessimistic	−100.0	−98.2	−61.3	—	0	7.7	45.2
	Optimistic	2852.0	260.1	130.1	—	0	−43.9	−893.5
	Actual	1517.0	−33.6	−50.7	—	0	−14.7	−86.6
	Avg.[a]							
Troller group	Low	−23.6	−36.9	2.4	—	−70.4	−64.6	−101.5
	Mid.	36.5	11.3	6.6	—	−7.9	−9.6	11.4
	High	25.0	7.6	8.5	—	81.1	75.3	93.4
	All[a]							

[a]Denotes scenario values for Table 5 results.

Consequently, the benefits to net worth are realized over the long term, making these investments attractive at a certain distance from the end of the planning period. When the planning period is short, e.g. 3 yr, license investments do not have enough time to build up benefits on the terminating net worth to warrant investment. However, for longer planning periods, e.g. 7 yr, license investments dominate all other types in the beginning years. In actuality, the purchase of new licenses often means that a change is required in fishing operations and skills, i.e. new areas are now open to fishing, or new fisheries are now available (e.g. herring). In such cases it takes some time before fishermen become efficient, learn the new skills, or familiarize themselves with new fishing grounds. Once this initial learning period has passed the net effect on the operation is a positive economic one.

More investments occur in type 2 capital (vessels) than in any other. Moreover, investments in vessels occur in all scenarios analysed. In comparing the parameters of the investment-income effects model, vessels have a more positive initial effect (q_0^2, q_1^2) than licenses, but this effect is more heavily discounted (ρ_2). Thus, vessel investments make a larger and more immediate impact on net worth. A consequence of this is higher investment in the interim years of each planning period.

The pattern of model investment in type 3 capital (gear/electronics) is likewise a function of its investment-income effects parameters. These investments make a more immediate impact on net worth, since they occur near the end of each planning period. This is a result of higher initial effects on income earning power (through q_0^3 and q_1^3) tempered by faster deterioration over time through ρ_3 (relative to ρ_1 and ρ_2).

Changing the survivability factor, p_0, only slightly effects model investment. For example, the types and patterns of investment remain the same as p_0 ranges from 0.0 to 0.1. The size of new investments increases marginally as p_0 increases, reflecting the greater willingness to invest by decision makers with higher risk positions. The effects on the average annual cash and net worth positions due to differences in p_0 alone are not dramatic (Table 6).

Investment model results by capital type given in Fig. 2 indicate that investment is highly sensitive to changes in the anticipated level of annual net operating income over the planning period. When income expectations exceed a minimum (or "pessimistic," Table 6) value approximately equal to the

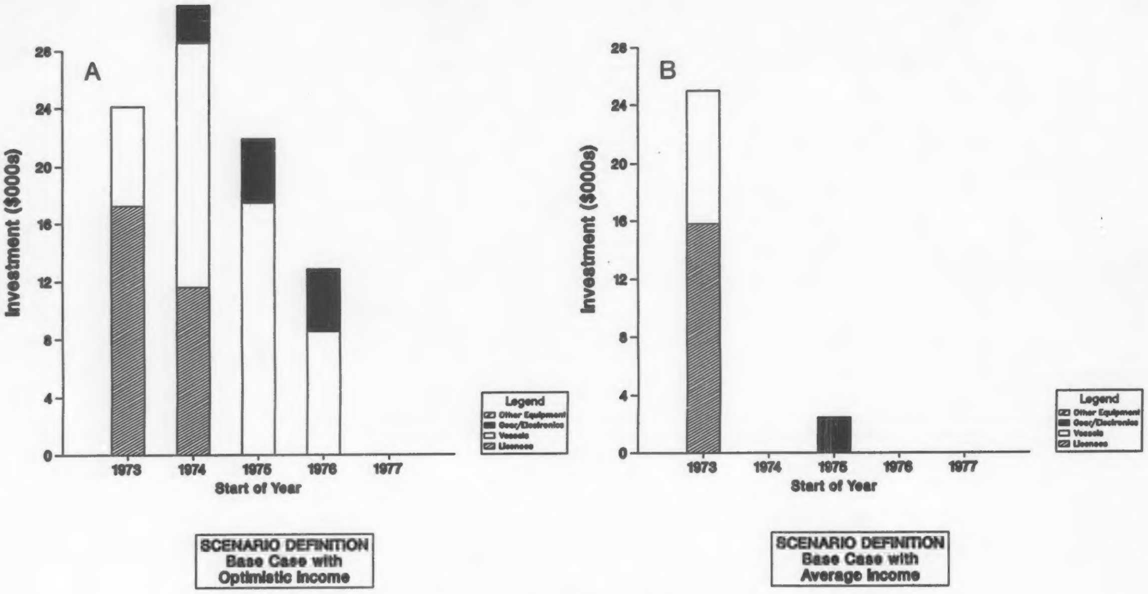

FIG. 2. Investment model results by capital type.

average level of annual obligations outstanding for trollers, then new investment takes place. At higher (or "optimistic") levels of anticipated income, a significant increase in investment occurs. Moreover, average annual cash and net worth positions fall with higher income expectations, *ceteris paribus* (Table 6).

When anticipated income is set to the actual average values over the planning period the pattern of investment is very different. In this case, model investments occur at the beginning of only two years, 1973 and 1976. These are the years of highest actual average income over the planning period. Investment is significantly increased in licenses but cut back in vessels and gear and electronics relative to base case investments. The result is a marginal decrease in the average annual net worth position of the troller group vis-à-vis the base case values of Table 5.

The investment patterns for different troller groups, namely, low and high fishing income earners, are comparable with those for different risk factors. Low earners, being affected by a less advantageous net worth position, invest less than middle or high earners in spite of the attractive anticipated income to the members of this group. Conversely, high income earners (as a consequence of their more secure net worth positions) invest more in spite of the less attractive anticipated income level to the trollers of this group.

The results of scenarios with planning periods of 3 and 7 yr show that when the shift in years relative to the base case scenario (5-yr planning period) is accounted for, the pattern of model investment is similar among all planning periods. Specifically, the 3-yr scenario investments are similar to that of the last three years of the base case results. The final 5 yr of the 7-yr planning period investments are likewise similar to the 5-yr base case results of Table 5. In the 7-yr scenario the initial 2 yr have significant investments in licenses reflecting the greater benefits to expected net worth at the terminating year of this longer planning period.

Model versus Actual Results

Actual average annual investment by capital type for 100 trollers from 1973 to 1982 is obtained from the troller annual cash report database (Fig. 3A). Model results were obtained by first "tuning" parameter values of the input data. In particular, the investment-income effects parameters were initially set equal to the empirically derived values (Table 5), the planning period was fixed at 4 yr, the survivability factor, p_0, was set to 5.0%, and the anticipated annual net operating income for each year of the first planning period (beginning in 1973) was set to $8500. Updating of the investment decision rule was assumed to occur after every year, i.e. average actual net operating income for the current year was averaged with the current anticipated net operating income value (at the beginning of the same year) to result in a new anticipated annual net operating income value for the upcoming years. This new value was then used to determine a new investment decision rule for the remainder of the planning period. Annual updating and new policy development continued from 1973 to 1982. The average annual investment per troller generated from the above procedure was then compared with the actual values for the same period. From the sensitivity analysis, model investment differences from year to year depend heavily on the updating of the anticipated net operating income (Fig. 2). Accordingly, discrepancies between model versus actual average investment can be corrected by adjusting anticipated income to replicate the actual investment response. (Different procedures for "tuning" the model may also be explored, including *n*-period moving average income calculations, constant income values (i.e. no updating), average growth rate income values, or specific patterns of income. As well, other model inputs may be varied such as the length of the planning period, the survivability factor, or the investment-income effects parameters.)

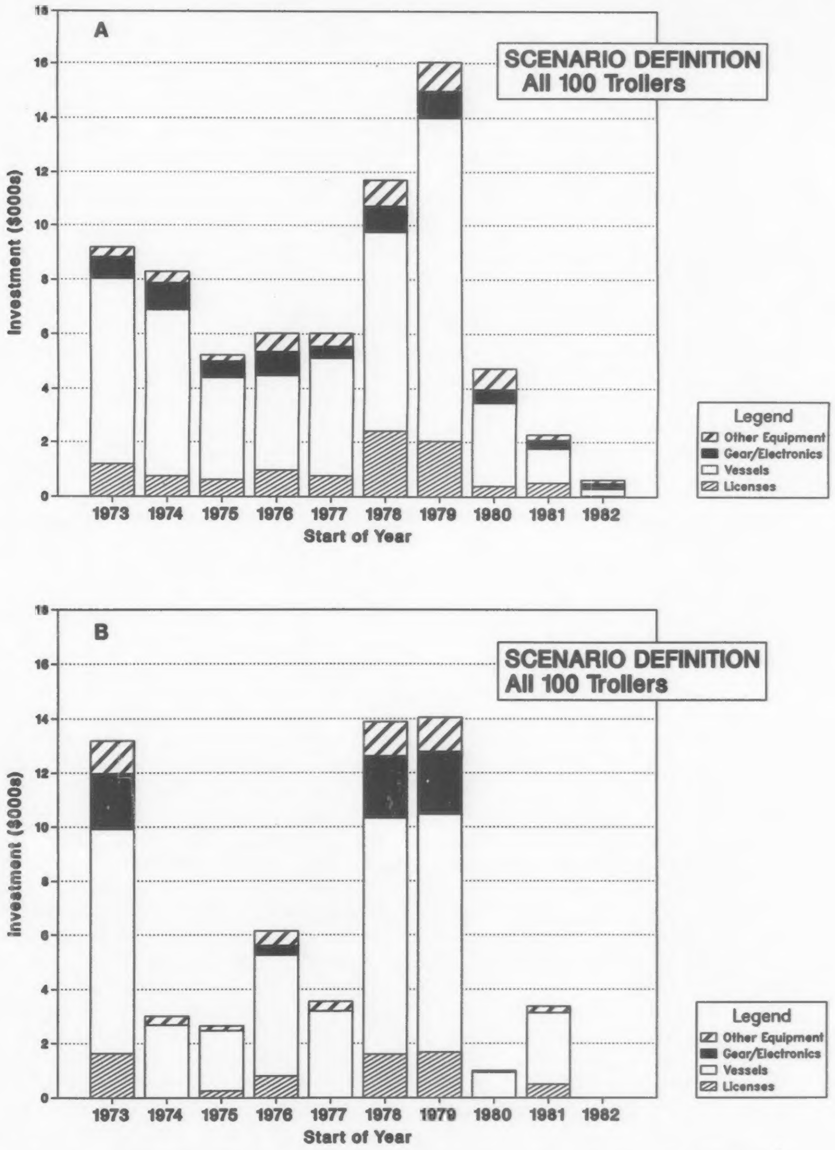

FIG. 3. (A) Actual and (B) predicted average troller investment by capital type (all 100 trollers).

The results of the comparison of model (Fig. 3B) versus actual investment (Fig. 3A) illustrate the ability of the model to replicate the real system through an appropriate tuning process. Predicted model values compare favorably with actual total investment (summed over all capital types). The correlation between actual average total investment and corresponding model results is 0.86. The annual mean absolute deviation (MAD) is $2300/yr on actual average investment totals of $7000/yr. Comparison of investment by each capital type for all 100 trollers shows that model investments are biased downward for type 1 capital (eligible capital) and type 2 capital (vessels). Type 3 investments (gear/electronics) have slightly positive bias, while type 4 investments (other equipment) are essentially unbiased over the 10-yr period. The MAD by capital type is largest for type 2 capital ($1800/yr), in which actual investment is greatest. MAD statistics for types 1, 3, and 4, respectively, are $449, $728, and $264/yr.

Specific groups of trollers were also examined and differences in actual and model results noted. Observations on investments made by middle income earners (trollers who earn annual gross income between 25 and 75 percentile of all trollers in the database) versus model results are similar to the all trollers group comparison. The correlation for total average annual investment is 0.95 with a MAD of $2200/yr on actual average total investments of $7100/yr. Analysis of investment by each capital type shows a slight negative bias in model results compared with actuals.

For trollers whose gross income ranges in the top 25 percentile of trollers in the database, the anticipated net operating income was initially set at $12 000/yr which is in line with the actual net operating incomes of trollers in this group. The largest discrepancy occurred in type 2 investments (MAD = $5110/yr) where actual investments are abnormally high in 1974 and 1979.

Actual average investment by low income trollers whose incomes are in the bottom 25 percentile shows an uncharacteristic smoothness over 1973–82 relative to other troller income groups. This suggests that investment by this group depends less on fluctuations in actual income. For example, average net operating income in 1975 for low income trollers was less than $50. This amount certainly does not cover average outstanding debt for 1975 estimated at $3000/troller. Yet, average actual investments in 1975 and 1976 remained at roughly equivalent levels amounting to over $4000/yr. Only in 1982 does actual investment differ substantially from that of all previous years. For model investments, the anticipated net operating income was set at $3000/yr for trollers of this group, approximating their actual income level. Model investments, however, fluctuate as a function of actual and updated anticipated incomes.

From the comparison of actual and model investments, insight may be acquired about the actual decision processes of the different troller groups. The above results suggest that each troller group segregated by income behaves quite differently with respect to investment decision making. For example, low earners appear to be overly optimistic about future earnings even when current incomes approach zero. They do not appear to adjust their investment strategies to take account of the actual swings in fishing income. Accordingly, they can build up debt loads which could become critical after a series of low income years. In fact, the expected net worth of an average low income earning troller operation followng the actual average investment strategy for the group from 1973 to 1981 approaches zero by 1981. This precarious situation actually resulted in the liquidation by bankruptcy of many trollers during 1981–82.

Actual investment by high income earners, on the other hand, follows a pattern of large investment in a single year followed by a series of years with no substantial investment. Peak investment periods (e.g. 1974 and 1979) are followed by sharply reduced investment years. It is interesting to note that the investment peaks occur after a sustained period of high income years, e.g. substantial investment takes place in 1974 after good incomes from 1972 to 1974; likewise, the 1979 investment spike occurs after good incomes were experienced from 1977 to 1979. Based on these observations, high income earners appear to be less myopic about anticipating future incomes. When income expectations are reinforced by a series of good years, then the result is an investment splurge. In comparison with the results of the investment model, this actual strategy contributes to reducing the expected net worth of the average high income earning troller at the end of 1982.

Discussion

The investment model begins with a simplified description of the net worth of the fishing enterprise. Different capital types are defined with associated financing arrangements. The key component of the model is the definition of functions relating investment and income. The risk of survivability is explicitly considered in a dynamic framework where updating of investment strategies may take place. Behavioral elements of the model are tuned to investigate aspects of actual investment trends among groups of commercial trollers. The importance of the model is in its ability to anticipate actual investment trends by fishermen.

The sensitivity analysis of this model illustrates the key role of income expectations on investment decisions. In fact, the evolution of the British Columbia salmon fishery since 1969 and licence limitation can be viewed as a series of modulating expectations which parallel investment trends. The 1969 Davis Plan also contained provisions for a buy-back programme. As a result, salmon fishing became more concentrated and the net worth of the remaining enterprises immediately increased. High prices for salmon in the early 1970's, the emergence of the roe herring fishery, and "loose" regulation, e.g. for vessel replacement rules, contributed to significant new investment buoyed by high future income expectations. Coincidentally, these events caused the termination of the buy-back programme due to sharply increasing vessel values and limited funds. In 1975, a poor harvest aggravated by a fishermen's strike clouded income expectations and investment fell off. By 1977, real prices were approaching pre-1975 levels. As well, a comprehensive salmonoid enhancement programme (SEP) was implemented and income expectations rose once again. Record high fish sales in 1978 and 1979 resulted in extraordinary new investment which was followed by ever-stricter vessel regulations. Late in the 1979 season, however, prices began to fall off sharply. From 1980 to 1982, market demand for salmon and herring fell dramatically as part of the worldwide economic malaise. The high income expectations of the late 1970's were not realized and consolidation occurred with actual net new investment in 1982 falling below zero. The plight of fishermen during this "down" period for fish prices precipitated the formation of the Pearse Commission in 1981. In recent years, fish markets have recovered and a new round of high expectations for the future and increased investment is now taking place in the commercial fisheries in British Columbia.

Based on the observations about the past and investment model results, it is clear that if income expectations could be "controlled," then investment would be affected directly. Moreover, the variability of income from year to year suggests that trollers' income expectations for example depend heavily on the current period's actual income. Accordingly, by affecting current income, income expectations are also affected. As suggested elsewhere (Pearse 1982), a landed value tax could be an efficient mechanism for achieving control of investment decisions. Moreover, within-season fleet dynamics and between-season investment decisions make this price regulation scheme a natural one in this setting (Lane 1986). The investment model can be used to quantify the expected impact of this regulation scheme on fishermen's investment decisions and the results of these decisions, e.g. on the economic value of their fishing operations under various conditions.

Capital investment in the model is restricted by the classification of investments for tax purposes. Each class includes investments which may or may not be directly related to increased fishing and earning power. For example, some investments are directed at increasing safety, comfort, and prestige (Hilborn and Ledbetter 1985). These investments may not contribute directly to increased earning power. Under current means of accounting for investment, it is impossible to identify the precise designation and use of purchased capital. More comprehensive databases are required before this issue can be adequately addressed.

The investment model is designed for modelling the decisions of fishermen within a particular class of capital, e.g. trollers. The consequences of major upgrading investments, for example whereby the fishermen moves to a new category of capital, are not captured in the current analysis. The move from a troller to a salmon seiner for instance takes the fishermen out of one homogeneous investment group and into another which may have different income and future investment characteristics. The approach in this analysis is to treat each of these groups separately and to model their within-group investment behavior only.

The empirical results for trollers of the British Columbia commercial fishing fleet give an indication that the model can be useful in predicting investment trends and potential under varying conditions. As an extension of this model, the investment potential of the secondary (processing) sector of the fishery can be similarly examined. The dynamic investment behavior also takes place in a related environment where survivability is a primary consideration.

The investment model attributes differences in seasonal incomes among fishermen to differences in their capital structure only. No within-season variation is attributed to motivational considerations or differences in skill between competing fishermen. The limited license fishery resulting in a ''closed shop'' of experienced trollers and the nature of the troll fishery itself are intuitive reasons for not including the skill factor explicitly as a determinant in explaining within-season income variations among fishermen.

In the model, individual fishermen behave as independent decision makers operating in a competitive environment. As such, the collective action of independent operators does not imply that the welfare of all fishermen is maximized simultaneously by this action. Wilen (1985) demonstrated this by a zero-sum game representation of fishermen–investors competing for a share of total allowable catch. The model is an example of the ''prisoners' dilemma'' whereby collectively it is better to cease investment and agree to share the catch. However, it is always to an individual's advantage to invest in a competitive environment to improve one's own position. Collective behavior by many individuals acting for their own benefit actually degrades everyone's economic welfare and leads to investment spiralling as a means of maintaining a share of a total allowable catch. A potential use of this model is in quantifying the effects of individuals' collective behavior. These results can then be compared with socially optimal strategies. In this way, measures of the cost of overcapacity in terms of the estimated loss of economic value of the fleet as a whole may be determined.

A primary purpose of this paper is to understand and incorporte the fisherman at the centre of the decision making process affecting his/her own destiny in the fishery. While implications about the actual behavior of fishermen can be drawn from model results, verification of these implications can only be determined by ''getting inside the heads'' of the fisherman decision maker. To this end, there can be no substitute for interviewing individual fishermen. The role of a decision making model of the kind proposed here provides a focus for the collection of more practical empirical data. With more data, firmly grounded in a better understanding of the behavioral aspects of investment through the modelling analysis, we will be in a much improved position to evaluate the impact of proposed new schemes aimed at stabilizing and ensuring a viable future for the fisheries and for fishermen.

Acknowledgements

The author gratefully acknowledges the support of Professors Ilan Vertinsky, Shelby Brumelle, Colin Clark, Don Ludwig, Marty Puterman, and Gordon Munro at the University of British Columbia for comments on previous drafts of this research which have substantially improved its content and presentation. The author also thanks Roy Mendelssohn, Douglas White, Marc Mangel, and an anonymous referee for their insightful comments and the Department of Fisheries and Oceans, Pacific Region, for the use of the data. This research was supported by NSERC team grant A6799.

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Factors Influencing Egg Extrusion in the American Lobster (*Homarus americanus*)

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Nelson, K., D. Hedgecock, and W. Borgeson. 1988. Factors influencing egg extrusion in the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 45: 797–804.

American lobster (*Homarus americanus*) females characteristically extrude eggs in the summer of the year following a summer or autumn molt, but young females may extrude in the same year. Adult female lobsters were exposed to periods of 40, 80, or 120 d of short photophase (8 h light : 16 h dark) at different times during the molt cycle or as controls were kept under continuous long-day conditions (16 h light : 8 h dark). They were found to require 80 d of short photophase to complete primary vitellogenesis; they then completed secondary vitellogenesis and extruded following long day onset (LDO) only if the latter fell within ±1400 dd_6 (day-degrees above 6°C) of the molt. The dependence of this latter relationship upon prior delayed extrusion and molting suggests that the decay in probability of LDO-elicited extrusion following the molt proceeds independently of the advance of the current molt cycle. The hypothesis is therefore rejected that the decay in extrusion potential following the molt is a result of increasing probability of interference from the oncoming premolt. Alternative hypotheses are discussed.

Les femelles de homard (*Homarus americanus*) pondent généralement l'été de l'année qui suit une mue d'été ou d'automne, mais les jeunes femelles peuvent pondre la même année. Des femelles adultes ont été exposées à une photopériode à courte phase éclairée (8 h de lumière : 16 h d'obscurité) pendant des périodes de 40, 80 ou 120 j, à divers moments du cycle de mue; les femelles témoins étaient maintenues dans des conditions de longue phase éclairée (16 h de lumière : 8 h d'obscurité). On a trouvé qu'il fallait 80 j à courte phase éclairée pour que s'accomplisse la vitellogenèse primaire; les femelles connaissaient alors leur vitellogenèse secondaire et pondaient après le début de la période à longue phase éclairée, à condition que celle-ci se situe dans une limite de ±1 400 dj_6 (degrés-jours au-dessus de 6°C) après la mue. La dépendance de cette relation à l'égard du retard dans la ponte et la mue indique que la baisse de probabilité de la ponte stimulée par le début de la longue phase éclairée après la mue est indépendante de l'avance du cycle de mue en cours. On rejette donc l'hypothèse selon laquelle la baisse du potentiel de ponte serait due à une augmentation de la probabilité de l'interférence causée par l'arrivée de la prémue, et on analyse d'autres hypothèses.

Received November 10, 1986
Accepted January 12, 1988
(J9008)

Reçu le 10 novembre 1986
Accepté le 12 janvier 1988

Growth and reproduction in decapod Crustacea as in other organisms have been thought to be antagonistic processes (Adiyodi and Adiyodi 1970; Hartnoll 1985). In those crustacean species in which molting continues throughout the reproductive life, the characteristic pattern is that in whch one or more clutches of eggs are produced during a more or less well-defined breeding season, almost always with successive molts intercalated between clutches (Hartnoll 1985). *Homarus* lobsters represent an extreme variant of this pattern. Reproductive maturity takes 5–8 yr. In the American lobster (*Homarus americanus*), the female reproductive cycle in nature typically lasts a full 2 yr (Aiken and Waddy 1976, 1980). The adult female molts and mates in late summer, extrudes eggs the next summer, and carries them on her pleopods until they hatch in the late spring or summer of the following year. Late that summer she molts again and the cycle may be repeated. Younger females may molt and extrude in the same summer and fall (Aiken and Waddy 1976).

However, the proportion of ovigerous females in the catch is generally lower than anticipated from the proportion of mature females and the duration of the ovigerous period (Herrick 1911; Uzmann et al. 1977; Ennis 1980; Campbell and Pezzack 1986). Among the hypotheses that may be entertained to explain this discrepancy is interference with reproduction by events associated with molting (Ennis 1980). The nature of the synchronization of the two processes and equally of their possible antagonism in the lobsters has been obscure (Aiken 1980; Nelson et al. 1983; Byard and Aiken 1984). We found with Massachusetts lobsters in our laboratory that photoperiod played a role. Females could be maintained in short days (short day period (SDP), 8 h light : 16 h dark) indefinitely without extruding; upon exposure to long days (long day onset (LDO), 16 h light : 8 h dark), a large proportion would extrude. On the other hand, females kept under continuous long days almost never extrude. The response to LDO varied with the timing of the molt (Nelson et al. 1983). At laboratory temperatures, egg extrusion followed LDO in approximately 120 d unless a molt intervened: if the molt occurred within 40–100 d after LDO, extrusion was delayed until about 80 d after the molt, but if the LDO–molt interval was greater than 120 d, extrusion was postponed indefinitely or until another SDP intervened. Following Aiken and Waddy (1976, 1980), we suggested that the possible antagonism between the processes might be expressed as interference by the events of premolt with the secondary vitellogenesis occasioned by LDO.

In the present study we take advantage of the vitellogenic response to photoperiod to test this hypothesis by varying the timing of LDO with respect to the molt. We also test the hypothesis that SDP of a certain duration is sufficient for LDO to elicit a vitellogenic response. Preliminary results were reported in Nelson (1986). The present paper revises these and examines the role of temperature in modifying the relationships between photoperiod, molting, and extrusion. A day-degree metric (dd_α, the sum of the daily temperatures above α°C between two events) is introduced and compared with the temporal metric measured in days (d). We also examine whether or not the occurrence of extrusion is influenced by the "organismic" independent variables of previous molting and reproductive history and individual variation, as well as by the environmental independent variables of photoperiod and temperature.

Materials and Methods

Experimental Subjects and Holding Conditions

Subjects were 99 adult female *H. americanus* obtained in December of 1976–80 from the Massachusetts inshore population (Tracey et al. 1975) and maintained and monitored in the laboratory for at least one full molt cycle (defined as running from one molt to the next) prior to entry into the experiment. Their average carapace length (measured from orbit to posterior carapace edge) at entry into the experiment was 97.6 ± 6.9 mm (variation is given as the standard deviation unless otherwise specified). They were housed individually in partitioned troughs, in semirecirculating seawater systems described previously (Hand et al. 1977). Individual compartment volume varied from 20 to 40 L, approximately in accordance with female size. One system was maintained on SDP (illumination during photophase from standard 70-W overhead fluorescent fixtures) at 14.3 ± 1.5°C (uncontrolled; several degrees above Bodega Bay ambient seawater temperature). One LDO system was kept at 15.9 ± 1.2°C (uncontrolled) and two systems, one a hatchery, were maintained at 19.0 ± 0.6°C (heated) to accelerate molting and reproductive cycles. Animals were fed a daily varied diet of fish and invertebrates on a basis of approximately 2.5% body weight per day. Frass and uneaten food were removed weekly or more often as needed. Temperature, molting, and premolt aphagia were recorded daily, and presence of eggs and gross morphological signs of impending molt were recorded weekly. Throughout most of the experiment, pleopodal "cement" gland stage (Aiken and Waddy 1982; scored in situ, however), indications of ovarian resorption (venter green), and the status of clutch, if present, were noted approximately every 4 wk, in all cases by the same experienced observer. Handling and disturbance were otherwise kept to a minimum, and no intrusive procedures were practiced except when necessary for disease diagnosis. Similarly, in this long-term study we elected not to employ setal-development molt staging (Aiken 1973) which in the lobster involves removal of a piece of pleopod for each examination.

Molted females were mated in 40- to 80-L compartments at the holding temperature as described in Nelson et al. (1983). Females experienced an overall mortality of 22% per year. Most deaths occurred during or soon after the molt, either from attack by the male during an attempted mating or from interference with molting by integumental lesions caused by chitinolytic bacteria (Fisher et al. 1976) or *Fusarium* (Lightner and Fontaine 1975). Data from severely infected females were discarded.

Experimental Protocol

All females had been held for at least 150 d in long-day pretreatment conditions. They were transferred from long days to short days at different times with respect to the time of molt, where they remained for either 40, 80, or 120 d (SDP) before being returned to a long-day system (LDO).

A control group (none of which had extruded eggs during its previous molt cycle) was maintained on long-day photoperiod throughout a molt cycle. Analysis of the relationship of intermolt interval to average temperature and size of female in this nonextruding control group (Nelson et al. 1988a) suggested expressing intervals both in days (d) and as the sum of day-degrees above 6°C (dd_6), the latter to incorporate the effect of varying temperature in phase comparisons.

Four years of experimental data from an average of 2.30 ± 0.77 completed molt cycles per female form the basis for the present report. Molt–LDO intervals were approximately normally distributed with a mean of 1112 ± 446 dd_6; 70% of LDOs were between 600 and 1400 dd_6 postmolt and 14% were between 1400 and 600 dd_6 prior to the next molt. These are the periods of the molt cycle of most interest, in which probability of extrusion rapidly changes. No transfer from short to long days occurred within ± 200 dd_6 of the molt, nor from long to short days while a female was ovigerous (and typically resident in the nursery system until after hatching).

Statistical Methods

One of the purposes of the study was to observe the effects of events of the previous molt cycle upon subsequent molting and reproduction. It was desired to utilize as much of the information gathered as possible, sometimes including data from several molt cycles by the same female in a given experimental category. Such data are by definition not independent, but we can estimate the contribution to the variance of our results by identity of female per se as an independent random-effects factor, as opposed to such female-associated fixed-effect variables as carapace length and occurrence of extrusion in the previous molt cycle.

We first test whether there is appreciable variance among females in probability of extrusion, the dependent variable of most interest in this report. It can be shown that were this the case, there should be more short and long strings of extrusion-containing molt cycles and fewer strings of intermediate length than expected from the hypothesis of homogeneity in extrusion transition probability among the ensemble of females:

$$f_i = nP^{i-1}(1-P), 0 < P < 1$$

where f_i is the expected frequency of extrusion molt cycle strings of length i, n is the total number of strings of extrusions, and P is the observed overall transition probability that a molt cycle with an extrusion will follow one with an extrusion (see Kemeny

TABLE 1. Effect of duration of short-day period (SDP) on frequency of extrusion. Females in the three SDP categories all experienced long-day onset (LDO) within ±900 day-degrees of molt.

	n	*n* extruding	% extruding
No SDP (control group)	28	0	0
40-d SDP	15 (12)[a]	3 (0)[a]	20 (0)[a]
80-d SDP	23	20	87
120-d SDP	25	21	84

[a] The three extruders received a 40-d SDP at the *end* of one molt cycle and another 40-d SDP at the *beginning* of the next, with less than 80 d of long days intervening.

and Snell 1960). Alternatively the expected distribution of strings of nonfertile molt cycles may be calculated from the corresponding transition probability.

We also tested to what extent identity of female per se contributed to the variance of other dependent variables within an experimental category. In appropriate tests of interval duration (dd_6) or of molt increment (millimetres) (by ANCOVA, regressed on size and other independent variables; Nelson et al. 1988a), female identity was included as an independent random-effects variable.

For ease of presentation we define a *positive LDO delay* as a molt–LDO interval followed by extrusion before the next molt. Temperature dependence of the decline in the proportion of positive LDO delays with an increase in their duration was investigated by both nonparametric and parametric statistical methods. First, we reasoned that the proportion of the variation in positive LDO delays that was due to temperature variation should be minimized if the molt–LDO intervals were measured in dd_α, day-degrees above α, the physiological zero for the process underlying the decay in probability of extrusion.

The *relative slope* of the decline in proportion of positive LDO delays was defined as the difference between the molt–LDO intervals corresponding to 75 and 25% extrusions divided into the 50% interval:

$$\text{Relative slope} = \frac{D_{50}}{D_{75} - D_{25}}$$

where D_p is the molt–LDO interval (dd_α) corresponding to the percentage p. The molt–LDO intervals were tabulated successively in terms of dd_α (e.g. dd_0, dd_1, dd_2, ...)for increasing integral values of α, and for each tabulation the relative slope was obtained graphically from the smoothed cumulative distributions.

Second, a parametric estimate of the appropriate day-degree metric was obtained by a similar maximization of the ANOVA difference between the distributions of the molt–LDO interval followed and not followed by extrusion, where the difference was defined as the ratio of the among- and within-group mean squares (F) for each day-degree tabulation.

Results

Effect of Variation Among Females

The distribution of length of strings of molt cycles with extrusion was not different from that expected from the transition probability model given under Materials and Methods ($P = 0.241$; $\chi^2 = 1.542$, df 2, n.s.), nor was the distribution of strings of molt cycles without extrusion different from that expected ($P = 0.301$; $\chi^2 = 3.618$, df 2, n.s.; excluding 40-d SDP and continuous long-day molt cycles, none of which contained an extrusion, and treating death or other exit from the data set as a third, absorbing state; Kemeny and Snell 1960).

In none of the ANCOVAs in which female identity was included as an independent random-effects variable was a significant F-ratio found. Inasmuch as we were taking into account previous molting and reproductive history, we therefore treated data relating to successive molt cycles of the same female as otherwise independent.

Effect of Length of Short-Day Period (SDP)

Females receiving 80- or 120-d SDPs with LDO within ±900 dd_6 of the molt extruded at a high rate; females experiencing only 40 d of SDP or no SDP at all (the control group) did not extrude (Table 1). Three females happening to receive a second 40-d SDP within 80 d of the termination of an earlier one extruded as well (Table 1). These results suggested that the effect of SDP was cumulative, at least up to approximately 80 d.

Eighty- and 120-d SDP extruders appeared similar in all respects, including LDO–extrusion interval D (dd_6) (for molt–LDO interval <900 dd_6, $\bar{D} = 1378 \pm 200$ and 1419 ± 205 dd_6, respectively; $F = 0.27$, df 1,28, $p > 0.5$) and hatching success (44% of extruders in each group hatched eggs).

In Fig. 1 the course of pleopod cement gland development (Aiken and Waddy 1982) following LDO is shown for extruders (80- and 120-d SDP groups were similar and are combined) and for nonextruders from each of the three SDP duration groups. The curves for the 80- and 120-d SDP nonextruders are similar to one another (ANOVA of individual average pleopod indices, 0–140 d post-LDO; $F = 0.15$, df 1,36, n.s.). Both are significantly different from that for the 40-d SDP group (80-d nonextruders vs. 40-d group; $F = 4.54$, df 1,28, $p < 0.05$; 120-d nonextruders vs. 40-d group; $F = 5.69$, df 1,40, $p < 0.025$). Both are significantly different from the extruders as well ($F = 8.03$, df 1,47, $p < 0.01$; $F = 7.096$, df 1,59, $p < 0.01$, respectively).

Thus, following LDO, even nonextruders from the two longer SDP groups showed an increase in pleopod index to more than 2.5; cement glands of females given a 40-d SDP displayed little change. Figure 1 suggests that the response of extruders following LDO is almost immediate (within 20–40 d of LDO). Eleven such females prematurely transferred back to short days after as few as 40 long days extruded at the expected time.

The 40-d SDP and continuous long-day females are excluded from the subsequent analyses, and results from 80- and 120-d SDP groups, showing no differences, are combined.

Effect of LDO Molt Phase

Figure 2A demonstrates that as LDO approaches the time of molt the percent of females who will extrude in response (about 700 dd_6 *following* the molt) rises sharply from zero approximately 100 d prior to the molt. The percentage falls to zero more gradually as LDO is increasingly delayed past the molt (Fig. 2B). With delayed LDO, extrusion is delayed an equivalent amount (dd_6; regression of molt–extrusion interval y on molt–LDO interval x: $y = 1330 + 0.803x$; $r = +0.69$, $p < 10^{-4}$). Hatching success, as measured by embryo retention interval (dd_6), was independent of phase of LDO (correlation with molt–LDO interval (dd_6), $r = -0.061$, n.s.).

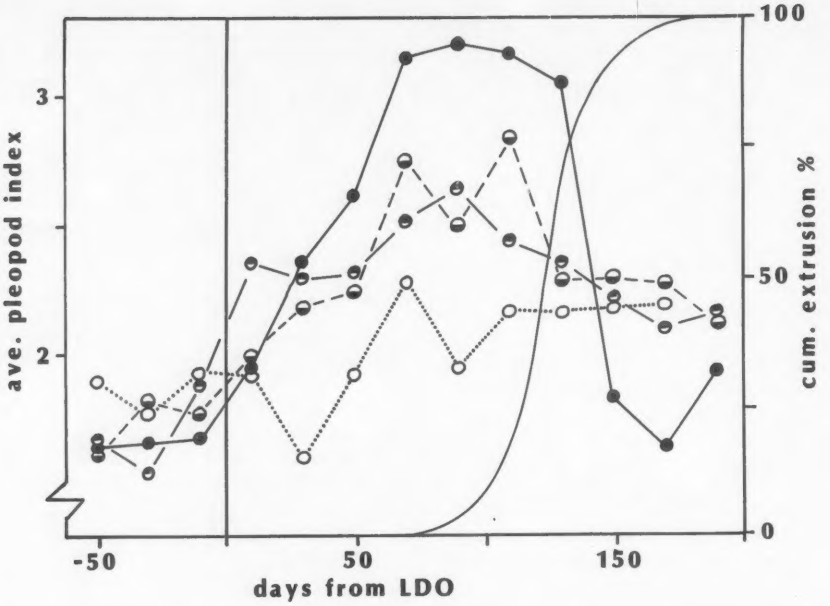

FIG. 1. LDO affects the reproductive physiology of females experiencing a short day photoperiod (SDP) of >80 d duration, even if they do not extrude. The course of average pleopod cement gland index as a function of time from long day onset (LDO). ● 80- and 120-d SDP extruders (smooth curve, smoothed cumulative distribution of LDO–extrusion intervals); ◓ = 120-d SDP nonextruders; ◒ = 80-d SDP nonextruders; ○ = 40-d SDP nonextruders. Average pleopod index for the long-day control group is 1.64 ± 0.61.

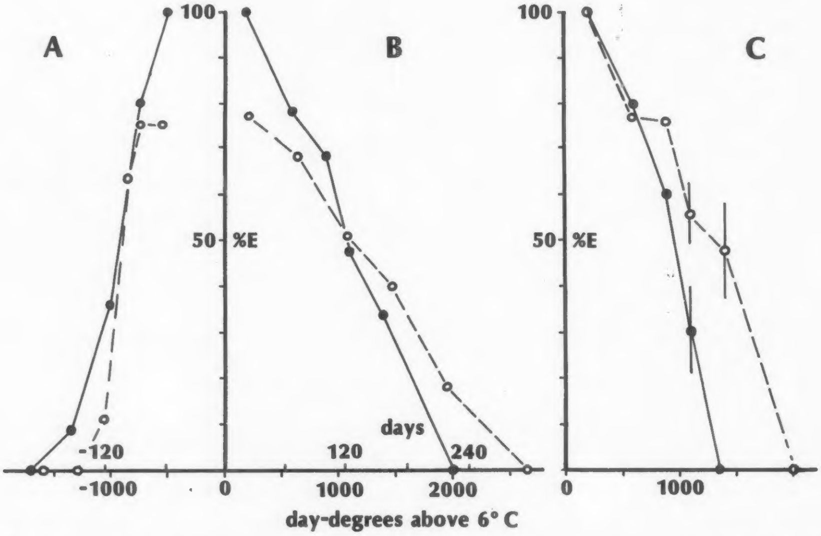

FIG. 2. (A) Percent of premolt LDOs leading after the molt to extrusion as a function of LDO–molt interval duration (○ = days; ● = day-degrees above 6°C (dd_6)). (B) Percent of postmolt LDOs leading to extrusion as a function of molt-LDO interval (○ = days; ● = dd_6). (C) Percent of postmolt LDOs leading to extrusion as function of molt-LDO interval (dd_6) (● = delayed extrusion in preceding molt cycle; ○ = no extrusion in preceding molt cycle). Standard errors are shown at points where curves differ significantly ($p < 0.05$).

TABLE 2. (a,b) Least-squares regressions of positive long day onset (LDO) delay (duration in dd_6 of molt-LDO interval followed by extrusion) upon previous intermolt interval duration (in days, as temperature record was often incomplete) containing or not containing extrusion. As assumptions of normality and homoscedasticity of residuals were not met, the nonparametric Spearman rank correlation coefficient r_s (Siegel 1956) is also given, with its associated level of significance. (c–e) Summary of analysis of covariance comparing the regressions for previous intermolt intervals containing and not containing extrusion. A similar dependence exists of positive LDO delay upon duration of previous intermolt interval with or without extrusion. a, intercept; b, regression coefficient; df, degrees of freedom; F, mean square ratio; p, level of significance; r, product-movement correlation coefficient; r_s, rank-order correlation coefficient; $\bar{x}$, variate mean.

	df	a	b	r	p	r_s	p
(a) Prior extrusion	24	1896	−2.3313	−0.530	<0.01	−0.592	<0.01
(b) No prior extrusion	44	1666	−2.0246	−0.531	<0.001	−0.494	<0.001

(c) prior intermolt interval (covariate)	$\bar{x}$	df	F	p
With extrusion	419.27 d	1,71	14.98	<0.001
Without extrusion	344.09 d			
(d) Molt–LDO interval				
Prior extrusion	920.3 dd_6	1,71	0.32	>0.05
No prior extrusion	963.74 dd_6			
(e) Residual mean squares		1,70	3.71	>0.05

Effect of Temperature Prior to LDO

The slope of the decline in positive LDO delays (molt–LDO intervals followed by extrusion) with increasing duration is steeper when the molt–LDO interval is measured in day-degrees (Fig. 2B). When the molt–LDO intervals were tabulated successively in terms of day-degrees above α for increasing integral values of α (e.g. dd_0, dd_1, dd_2, ...), the relative slope of the decline in positive LDO delays obtained showed a single sharp negative minimum at $\alpha = 6°C$. This slope is displayed in Fig. 2B. A similar value for α was obtained by maximizing in a similar way the difference between the distributions of positive and negative LDO delays ($F = 16.44$, df 1, 147, $p < 10^{-4}$, for $\alpha = 7°C$).

Data were too limited for a similar comparison of α values for LDOs preceding the molt (only 29 cases with LDO–molt interval in the range 0–1400 dd_6 in which elicitation of extrusion was possible enter into Fig. 2A, compared with 149 postmolt LDOs which are the data of Fig. 2B). Nevertheless, Fig. 2A and 2B together show that LDOs occurring within ±500 dd_6 of the molt may elicit extrusion 100% of the time.

Effects of Events of the Previous Molt Cycle

We demonstrate elsewhere (Nelson et al. 1988a) that if extrusion follows a delayed LDO, as in Fig. 2B, the subsequent molt is also delayed. Figure 2C indicates that the decline in positive LDO delays following the molt occurs 300–500 dd_6 "sooner" when such an LDO-delayed extrusion has also preceded, and therefore delayed, the molt.

Molt–LDO interval distributions following undelayed prior extrusions show no such reduction in duration of positive LDO delays, although there are too few data for adequate direct statistical test. But positive LDO delay is a decreasing function of preceding intermolt interval, whether or not the latter contains an extrusion (compare Table 2a and 2b). In the absence of extrusion the duration of the molt cycle is largely determined by female size whereas when extrusion is present, its delay largely governs time of the molt (Nelson et al. 1988a); thus, the extrusion-delayed molt cycle is generally longer (Table 2c). Nevertheless the two kinds of variation in molt cycle duration have similar effects upon the selection of positive LDO delays (Table 2e).

Discussion

The results of this study enable us to delineate the nature of the reproductive photoperiodic response in female *H. americanus* and to relate this response to its timing with respect to both the concurrent and the preceding molt cycles. We discuss these results separately.

Nature of the Photoperiodic Response

We demonstrate that whereas a 40-d SDP is insufficient to bring about egg extrusion, 80- and 120-d SDPs are, *ceteris paribus*, equally efficient (Table 1). It appeared that two 40-d SDPs can add to produce the effect of a single 80-d SDP. Females from our population extrude neither under conditions of continuous long days (our control group) nor in continuous short days (Nelson et al. 1983); they require the stimulus of LDO.

Females transferred back to short days after as few as 40 long days will nevertheless extrude, the extrusion occurring at the usual time following the original LDO. The nearly immediate rise in pleopod index following LDO (Fig. 1) suggests that an even shorter period of long days might be sufficient (incidental observations indicate one long day is not enough). LDO thus may serve more as a trigger than as a sustaining condition for this phase of vitellogenesis.

There is general agreement that vitellogenesis in malacostracan crustaceans can be divided into variously characterized primary and secondary stages (Meusy and Charniaux-Cotton 1984; Adiyodi 1985; Charniaux-Cotton 1985), and the American lobster appears to be no exception (Aiken and Waddy 1980). We surmise that short days sustain primary vitellogenesis until its completion and we have found that in this population, LDO triggers secondary vitellogenesis, as assayed by increasing hemolymph concentration of vitellogenins, which are immunologically identical with two major egg proteins (Nelson 1986; Nelson et al. 1988b).

This *H. americanus* pattern appears to be somewhat different from that found in another astacuran decapod, the crayfish *Orconectes*. In *O. virilis*, cold dark conditions appear to sustain the entire vitellogenesis, and warm water serves merely to trigger oviposition (Aiken 1969); in *O. nais*, short day length appears similarly to sustain all of vitellogenesis (Armitage et al. 1973). The two-phase photoperiodic response of *H. americanus* females is reminiscent of two-phase reproductive diapause development found in long-day insects of the genus *Pterostichus*, involving "a short-day requirement for previtellogenesis and a long-day requirement for the initiation of vitellogenesis" (Beck 1980).

There have been reports by Waddy and Aiken (1984) and Aiken and Waddy (1985, 1986) of absence of photoperiodic effect upon the timing of extrusion in Prince Edward Island *H. americanus* kept on a seminatural annual temperature cycle. We have discussed this elsewhere (Nelson and Hedgecock 1985; Nelson 1986). In our laboratory with only a small annual variation in temperature, Prince Edward Island females do respond to LDO by extruding (unpublished results). The possibility exists that in the extreme temperature regime experienced by this population in nature the photoperiodic response is suppressed or overridden by a temperature control; in unpublished pilot experiments we found no indication of an effect of a 6°C cold period of varying length and timing in either offshore or inshore Massachusetts lobsters. European lobsters (*Homarus gammarus*) and hybrids between the species extrude 70–120 d after the molt (Nelson 1986); there is no evidence for photoperiodic control. The differences between our results and those of Waddy and Aiken (op. cit.) may similarly reflect geographic variation in control of reproduction.

Vitellogenesis and the Molt Cycle

By manipulating the phase of LDO with respect to the molt, we found in essence that extrusions were triggered only by LDOs within ± 1400 dd_6 of the molt (Fig. 2). Within this range, if LDO occurred prior to the molt, extrusion followed that molt in approximately 700 dd_6; if LDO occurred after the molt, extrusion was delayed until approximately 1400 dd_6 after LDO. It is of critical importance that we ask how closely linked to the molt cycle are the controls governing this molt-associated peak in the probability that an LDO "probe" will be followed by extrusion. We will refer to this probability as LDO extrusion potential.

Several lines of evidence indicate that the failure following a too-long-delayed LDO is a failure to *sustain* secondary vitellogenesis rather than a failure to *initiate* it, for example due to a postmolt inhibition of primary vitellogenesis. As we have noted, the pleopod cement gland index, a predictor of extrusion (Aiken and Waddy 1982), responds to LDO following an 80- or 120-d SDP with an increase, although not with as large an increase when extrusion is not to follow (Fig. 1). Similarly, following an initial post-LDO decline, size of ovary as measured by a candling index increases in such anovulatory cycles parallel to its course in ovulatory ones, but does not become as large (Nelson 1986). Vitellogenin levels in these anovulatory cycles usually rise following LDO, often to the very high levels characteristic of resorbing ovaries (Nelson 1986; Nelson et al. 1988b).

One possibility is that the processes governing the development of premolt interfere in some way with vitellogenesis. In an earlier study, we postulated that a premolt beginning near LDO would interfere with the onset of secondary vitellogenesis, causing its delay until after the molt; interference from a premolt starting once secondary vitellogenesis had begun would result in ovarian resorption (Nelson et al. 1983). Byard and Aiken (1984) reasoned similarly about the outcome of an experiment in which desynchronization between vitellogenesis and the molt cycle was occasioned by an accelerated "annual" temperature/photoperiod cycle. We will refer to this hypothesis as the *premolt interference hypothesis*; among its advantages are that it might account not only for the decline in probability of extrusion following the molt (Fig. 2B) but also for the increase prior to the molt (Fig. 2A). According to Aiken (1980) and Chang and Bruce (1980), in the absence of extrusion, premolt begins at approximately the last 15–20% of the intermolt interval (i.e. for a 3000-dd_6 intermolt interval, approximately 450–600 dd_6 before the molt).

Elsewhere (Nelson 1986; Nelson et al. 1988b) we observed that when ovarian resorption occurred it usually began well prior to the beginning of the next premolt, suggesting some other mechanism for resorption than premolt interference. In other results from the present study (Nelson et al. 1988a) we noted that massive resorption as evidenced by a green venter was never initiated during either the first or the last 600 dd_6 of the molt cycle, but over an interval of about 2000 dd_6, its timing was independent of time of molt. Most anovulatory females show no evidence of massive resorption. Thus, whatever its significance, the *timing* of massive resorption need not be related to the timing of LDO with respect to the molt. The premolt interference hypothesis is a special case of a more general hypothesis, in which an event or process directly related to the advance of the molt cycle results in the cutoff in LDO extrusion potential: the *molt cycle advance hypothesis*.

The premature cutoff in LDO extrusion potential following longer intermolt intervals (Table 2) presents difficulties for any simple molt cycle advance hypothesis. When an intermolt interval is prolonged by female size or by a delayed extrusion, the following cutoff in extrusion potential is advanced with respect to the molt (Table 2); it is as if the process resulting in the cutoff in this case actually begins prior to the delayed molt. However, our very limited data do not suggest that the increase in LDO extrusion potential *prior* to the molt (Fig. 2A) is sooner before a delayed molt, but the answer to this must await further experimental study. Nevertheless, if the peak (Fig. 2A, 2B) in extrusion potential of LDO is tied to the molt itself, its tether is quite long. Strictly speaking, it appears to be incorrect to speak of the probability of LDO eliciting an extrusion as if it were a function of the phase of the current molt cycle.

Thus the failure to sustain secondary vitellogenesis when LDO is too long postponed appears strictly to be independent of the timing of both the preceding and the following molts, although perhaps not independent of the former in a more indirect sense. What could be the mechanism of such a loose coupling?

One possibility is that in the female *Homarus*, the putative molt-inhibiting and gonad-inhibiting neuropeptide hormones produced in the eyestalk complex (MIH and GIH or OIH) are identical, a "growth inhibiting principle" as suggested by Adiyodi and Subramoniam (1983). It has been difficult to prove that MIH and GIH are different, and even more difficult to demonstrate their separate control (Meusy and Charniaux-Cotton 1984). van Deijnen et al. (1984) have reported vitellogenesis-inhibiting ("GIH") activity from a fraction of *H. americanus* sinus gland extract quite distinct from the molt-inhibiting fraction. But the GIH assay species was a freshwater atyid shrimp; because of the evolutionary plasticity of neuropeptides, assay on a heterologous species cannot be considered decisive (E.S. Chang, Bodega Marine Laboratory, Bodega Bay, CA, pers. comm.). MIH level is supposed to decrease just prior to the advent of premolt, and to rise following the molt — the precise timing especially of the latter rise is unknown. The curves of extrusion potential would then be inversely related to the titer of "growth inhibiting principle."

Another possibility is that one or more organs involved in vitellogenesis require molting hormone (ecdysteroids, ECD) to sustain their function. Such an organ presumably would sequester ECD during its premolt peak titers and gradually lose it by degradation or leakage after the molt. There is both ample precedent and evidence of functional importance among the Malacostraca for a positive ovarian relationship between molting hormone and vitellogenesis (e.g. Blanchet-Tournier 1982; Lachaise and Hoffmann 1977).

Such hormonal explanations tied to the molt are difficult to reconcile with well-documented cases of multiple broods within an instar in very large lobsters (>120 mm carapace length and thus beyond the range of the present study; Waddy and Aiken 1986). Also, the effect of a previous delayed molt in shortening the period of postmolt LDO extrusion potential is explained no better by a molt-linked hormonal hypothesis than by a molt cycle advance hypothesis.

It seems inevitable that we must search for separate controls to explain the loose coupling of the processes. Steel (1980) came to a similar conclusion regarding the synchrony of molting and reproduction in the terrestrial isopod *Oniscus asellus*. A kind of separate control for probability of extrusion would be provided in a circannual rhythm (Saunders 1977) by which the timing of the next peak in LDO extrusion potential — but not that of the current peak — is reset at the current molt. Thus the absolute rather than relative timing of the cutoff — and perhaps also of the beginning — of the current peak would be a function of the timing of the previous molt. Such a circannual rhythm could account simply for the decrease in positive LDO delay with increase in intermolt interval (Table 2). In the prolonged absence of molting, as with a very large female, such a free-running rhythm might generate multiple peaks in LDO extrusion potential. This could account for the observations of multiple broods within the extended molt cycles of such females (Waddy and Aiken 1986).

In an accompanying paper (Nelson et al. 1988a), we follow the consequences of reproduction further. We show that the molt cycle next following an extrusion is shorter, whether or not it itself contains an extrusion, and also whether or not the prior molt was delayed. This latter finding is at variance with the decrease in positive LDO delay of Table 2. Thus although there are pervasive effects of prior extrusion both upon subsequent reproduction and upon the subsequent molt cycle, the processes underlying the advance in cutoff of LDO extrusion potential and the advance of the following molt are affected by disparate aspects of previous reproduction.

NOTE ADDED IN PROOF

Recent experiments by Waddy and Aiken (1987 and pers. comm.) have confirmed our suggestion that the photoperiodic vitellogenic response in Prince Edward Island lobsters is indeed similar to that in Massachusetts inshore lobsters, but that it is overridden by temperature in the natural northern inshore environment.

Acknowledgements

We thank John Hughes, former director of the Massachusetts State Lobster Hatchery, Vineyard Haven, for his cooperation in obtaining lobsters and E. S. Chang, Bodega Marine Laboratory, for his helpful suggestions on the manuscript. This project was supported by NOAA, National Sea Grant College Program, Department of Commerce, under project Nos. R/A45 and R/A65, through the California Sea Grant Program. We thank D. Cosgrove and C. J. Culp for preparing the manuscript.

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Effects of Reproduction upon Molting and Growth in Female American Lobsters (*Homarus americanus*)

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Nelson, K., D. Hedgecock, and W. Borgeson. 1988. Effects of reproduction upon molting and growth in female American lobsters (*Homarus americanus*). Can. J. Fish Aquat. Sci. 45: 805–821.

American lobster (*Homarus americanus*) females characteristically extrude eggs (E) in the summer of the year following a summer or autumn molt (M), but young females may extrude in the same year. The subsequent M is delayed until after hatching, resulting in the former case in a 2-yr reproductive molt cycle, measuring from M to M. Adult female lobsters were exposed to periods of short days (8 h light : 16 h dark) followed by long day onset (L) (16 h light : 8 h dark) at different times with respect to M, or as controls were kept under continuous long-day conditions. In this way were generated molt cycles with delayed or undelayed extrusions, as well as ones with incomplete vitellogeneses resulting from too-long delayed L, and molt cycles in which vitrellogenesis did not begin (control group). Delayed L results in delayed E and M, as measured either in days or in day-degrees above 6°C. An incompleted vitellogenesis following a too-long delayed L changes neither the duration of the molt cycle nor its characteristic positive correlation with female size; the duration of molt cycles containing either delayed or undelayed E appears in contrast to become independent of size. Intermolt intervals following prior E are shorter than those following anovulatory cycles. Retention of the clutch to hatching is associated with an additional increment to the intermolt interval. The results suggest that following E, a "reproductive" program replaces the "somatic" program of control of molt cycle duration. Incompleted vitellogeneses are associated with significantly smaller molt increments and growth rates than in the evidently avitellogenic continuous long-day control group, even though intermolt duration and its relation to size remain the same. Growth rates of molt cycles containing incompleted vitellogeneses are significantly higher than ones containing E only if that is delayed. Differential dependence of molt cycle duration and growth rate measures upon size and temperature indicate that molting and growth are distinct and rather independently controlled processes in adult lobsters, however tightly linked they may be in juveniles. Implications for molting and reproduction in the natural environment are discussed.

Les femelles de homard (*Homarus americanus*) pondent généralement l'été de l'année qui suit une mue d'été ou d'automne, mais les jeunes femelles peuvent pondre la même année. La mue suivante est retardée jusqu'après l'éclosion, de sorte que le cycle de mue et de reproduction peut durer 2 a. Des femelles adultes ont été exposées à une photopériode à courte phase éclairée (8 h de lumière : 16 h d'obscurité) pendant certaines périodes, puis à une longue phase éclairée (16 h de lumière : 8 h d'obscurité); les femelles témoins étaient maintenues dans des conditions de longue phase éclairée. Nous avons ainsi créé des cycles de mue avec ponte retardée ou non, et d'autres avec vitellogenèses incomplètes à cause du trop grand retard de la longue phase éclairée, ou encore sans démarrage de la vitellogenèse (groupe témoin). Le retard de la longue phase éclairée cause un retard de la ponte et de la mue, mesuré en jours ou en degrés-jours au-dessus de 6°C. La vitellogenèse incomplète suivant un trop grand retard de la longue phase éclairée ne change ni la durée du cycle de mue ni sa corrélation caractéristique positive avec la taille de la femelle; la durée des cycles de mue avec ponte retardée ou non semble par contre indépendante de la taille. Les intervalles entre les mues après la première ponte sont plus courts que ceux qui suivent les cycles sans ovulation. Le port de la ponte jusqu'à l'éclosion est associé à une augmentation supplémentaire de l'intervalle entre les mues. Les résultats semblent indiquer qu'après la ponte, un programme « reproductif » remplace le programme « somatique » qui régit la durée du cycle de mue. Les vitellogenèses incomplètes sont associées à des accroissements à la mue et à des taux de croissance nettement plus faibles que chez le groupe témoin, bien que l'intervalle entre les mues et sa relation avec la taille demeurent les mêmes. Les taux de croissance dans les cycles de mue avec vitellogenèse incomplète sont nettement supérieurs à ceux des cycles avec ponte, dans les cas seulement où la ponte est retardée. La différence dans la dépendance de la durée du cycle de mue et du taux de croissance à l'égard de la taille et de la température indique que la mue et la croissance sont des processus distincts et régis séparément chez les homards adultes, bien qu'ils soient étroitement liés chez les juvéniles. Les auteurs analysent les incidences sur la mue et la reproduction dans le milieu naturel.

Received November 10, 1986
Accepted January 11, 1988
(J9009)

Reçu le 10 novembre 1986
Accepté le 11 janvier 1988

The partitioning of resources between growth and reproduction has been achieved in various ways in different groups of Crustacea (Sastry 1983; Hartnoll 1985; Conan 1985). In those species in which molting continues to occur throughout adulthood, the usual pattern is the production of one or more clutches of eggs during a more or less well-defined breeding season, with one or more molts intercalated between clutches. In most Malacostraca the embryos are brooded on the abdomen, either attached to pleopodal hairs as in decapods or held in a brood pouch as in isopods. If the duration of incubation is appreciable, the duration of the molt cycle (i.e. from molt to molt) must be prolonged to accommodate it, lest the clutch be lost with the molt. Hartnoll (1985) discussed other possible reasons for prolonged ovigerous intermolts: partitioning of resources between growth and reproduction and restricted food intake during brooding, for example.

American lobster (*Homarus americanus*) females are extreme in these respects. Reproductive maturity takes 5–8 yr. The female lobster reproductive cycle typically lasts a full 2 yr (Aiken and Waddy 1980). The adult female molts and mates in late summer, extrudes eggs the next summer, and carries them on the pleopods until they hatch in the late spring or summer of the following year. Late that summer she molts again and the cycle is repeated. But younger adult females may molt and extrude in the same summer and fall (Aiken and Waddy 1976). Thus we can identify two patterns in the field: extrusion soon after molting and extrusion only after a long delay (see also Lipcius 1985). In the latter case, the intermolt interval must be greatly prolonged to accommodate both delayed extrusion and the nearly 1-yr-long incubation period characteristic of this species. Otherwise, the clutch — possibly a 2-yr reproductive investment — will be lost.

In an experiment in which we exposed female lobsters from the Massachusetts inshore population to short-day photoperiod (SDP) for varying lengths of time, with long-day onset (L) at varying times with respect to the molt (M), we were able to establish that SDP provided an appropriate environment for the early portion of vitellogenesis whereas L triggered secondary vitellogenesis and subsequent extrusion (E) (Nelson et al. 1988a). L was only effective in eliciting E within approximately ±1400 dd_6 (day-degrees above 6°C; see Appendix 1) of M.

Thus in this experiment we generated four groups of molt cycles (Table 1), those in which L occurring prior to M triggered E soon after M, those in which L delayed until well after M triggered a delayed E, those in which a too-long delayed L was ineffective in producing E, and those in which females kept in continuous long days also failed to extrude. The present study compares the effects of these four experimentally produced conditions of reproduction and nonreproduction upon molting and growth. We also report the effects of the uncontrolled adjunct variables of female size, temperature, presence of the clutch and prior reproductive history. We introduce a uniform terminology with which to discuss the complicated relationships between M, L, and E and discuss the implications of these relationships for lobster natural history.

Materials and Methods

Experimental Subjects and Holding Conditions

Subjects were 99 adult female *H. americanus* obtained in December of 1976–80 from the Massachusetts inshore population (Tracey et al. 1975) and maintained and monitored in the laboratory for at least one full molt cycle prior to entry into the experiment. Their average carapace length from orbit (l) at entry into the experiment was 97.6 ± 6.9 mm (variation is given as the standard deviation unless otherwise specified). They were housed individually in partitioned troughs, in semirecirculating seawater systems described previously (Hand et al. 1977). Individual compartment volume varied from 20 to 40 L, approximately in accordance with female size. One system was maintained on SDP (8 h light : 16 h dark; illumination during photophase from standard 70-W overhead fluorescent fixtures) at 14.3 ± 1.5°C (uncontrolled; several degrees above Bodega Bay ambient seawater temperature). One long-day system (16 h light : 8 h dark) was kept at 15.9 ± 1.2°C (uncontrolled) and two (one a hatchery system) were maintained at 19.0 ± 0.6°C (heated) to accelerate molting and reproductive cycles.

Animals were fed a daily varied diet of fish and invertebrates on a basis of approximately 2.5% body weight per day. Frass and uneaten food were removed weekly or more often as needed. Temperature, molting, and premolt aphagia were recorded daily, and presence of eggs and gross morphological signs of impending molt were recorded weekly. Throughout most of the experiment, pleopodal "cement" gland stage (Aiken and Waddy 1982; scored in situ, however), indications of ovarian resorption (venter green), and status of clutch if present were noted approximately every 4 wk, in all cases by the same experienced observer. Within 2 d of molting, females were mated in 40- to 80-L compartments at the holding temperature as described in Nelson et al. (1983). Approximately half of the matings were to conspecifics and half were to male European lobsters (*Homarus gammarus*). Sixteen matings were to hybrid males (*H. americanus* × *H. gammarus*), later confirmed to be infertile. Mated females were examined for external indication of spermatophore. During the study we were able to carefully match 10 pairs of females on the basis of size, dates of M, L, and E, and previous photoperiod, temperature, and reproductive history. Within 180 dd_6 of E, eggs of a randomly selected member of each pair were gently brushed off. Until their following molts, pair members were held under the same temperature and photoperiod to test whether presence of the clutch delayed M.

Handling and disturbance of females were otherwise kept to a minimum, and no intrusive procedures were practiced except when necessary for disease diagnosis. Similarly, in this long-term study we elected not to employ setal-development molt staging (Aiken 1973) which in the lobster involves removal of a piece of pleopod for each examination.

Females experienced an overall mortality of 22% per year, consistent with New England lobster natural mortality estimates (Anthony 1980). Most deaths occurred during or soon after M, either from attack by the male during an attempted mating or from interference with molting by integumental lesions caused by chitinolytic bacteria (Fisher et al. 1976) or *Fusarium* (Lightner and Fontaine 1975). Data from severely infected females were discarded. In particular, measures of molt increment G_M (the increase in carapace length following M) were discarded if the female had not survived well into her following molt cycle.

Experimental Protocol

All females had been held for at least 150 d in long-day pretreatment conditions. They were transferred from long days to

TABLE 1. Relationships among symbols used in the text.

A. Events

E	Egg extrusion
L	Long day onset
M	Molt
R	Removal or release of eggs or larvae

B. Dichotomies used to classify molt cycles

L–NoL	Long day onset present or not in *current* molt cycle i
E–NoE	Extrusion present or not in *current* molt cycle i
EPREV–NoEPREV	Extrusion present or not in *previous* molt cycle $i-1$
HATCH–SLOUGH	E–R interval greater or less than 1000 dd_6 (day-degrees above 6°C)
EFOL–NoEFOL	Early extrusion present or not in *next* molt cycle $i+1$

C. Classification of molt cycles used in analysis. Groups or subgroups compared are all those at the same level of the classification hierarchy; dichotomies not resolved in comparisons at that level are left blank. The number (n) in a subgroup is sometimes reduced because of incompleteness of animal's records (e.g. uncertainty of hatching date).

Group	Event sequence	n	Classification L?	 E?	 EPREV?	 HATCH?
1. NoL, NoE	MM	28	–	–		
2. L, NoE	MLM	75	+	–		
a. NoEPREV	MLM	43	+	–	–	
b. EPREV	EMLM	32	+	–	+	
3. NoL, E	LMERM	19	–	+		
a. SLOUGH	LMERM	7	–	+		–
b. HATCH	LMERM	9	–	+		+
4. L, E	MLERM	85	+	+		
a. NoEPREV	MLERM	57	+	+	–	
1. SLOUGH	MLERM	21	+	+	–	–
2. HATCH	MLERM	26	+	+	–	+
b. EPREV	EMLERM	28	+	+	+	
1. SLOUGH	EMLERM	8	+	+	+	–
2. HATCH	EMLERM	8	+	+	+	+

Growth comparisons only (Tables 6–8), L, NoE, $I_{LM} \leqslant 140$ *d*

Group	Event sequence	n	L?	E?	EFOL?
2. L, NoE	MLM				
a. NoEFOL	MLM	6	+	–	–
b. EFOL	MLME	7	+	–	+

D. Measures of duration and temperature

I_{XY}	Interval in days (d) between a preceding event X and a following event Y. Thus, I_{LM} is the interval between long day onset and the following molt
D_{XY}	Sum of day-degrees above 6°C (dd_6) between a preceding event X and a following event Y. Thus, D_{ME} is the day-degree sum between a molt and a following extrusion in the same molt cycle
(t, t_o, T, t)	Interval durations measured in years (yr) used in growth equations in Appendix 2
t	Temperature in °C
T_{XY}	Average temperature above 6°C between two events, X and Y
S_{XY}	T^{-1}, or the harmonic mean of the daily reciprocals of temperature above 6°C between two events, X and Y

TABLE 1. (*Concluded*)

E. Measures of growth	
l_i	Carapace length in mm, measured from rear edge of orbit, during molt cycle i
G_M	Molt increment, the increase in carapace length at the molt, $l_{i+1}-l_i$
G_{MM}	Carapace length growth rate in mm·yr^{-1} during a molt cycle, $365G_M/I_{MM}$
G	Estimated instantaneous carapace length growth rate, in mm·yr^{-1}, for a molt cycle (see Appendix 2)
k	Pütter – von Bertalanffy growth coefficient
L_∞	Pütter – von Bertalanffy asymptotic carapace length
E	$=kL_\infty$; initial growth rate in Pütter – von Bertalanffy equation (differential form)

TABLE 2. Mean $\bar{x}$ and standard deviation SD for interval durations measured in days (I) and day-degrees above 6°C (D) for molt cycle groups 1–4. $\bar{l}$ = mean carapace length; M = molt, L = long day onset, E = extrusion, R = egg or larvae release or removal (SLOUGH or HATCH). Groups are classified according to presence or absence of L and E during molt cycle.

	I (d)		D (dd$_6$)	
	$\bar{x}$	SD	$\bar{x}$	SD
1. NoL, NoE, $\bar{l}$ = 95.5 ± 4.8 mm, n = 27				
MM	299.0	70.4	2987	770
2. L, NoE, $\bar{l}$ = 99.3 ± 6.8 mm, n = 54				
MM	327.0	68.7	3083	728
ML	140.5	32.9	1214	326
LM	189.7	77.1	1843	788
3. NoL, E, $\bar{l}$ = 101.0 ± 8.7 mm, n = 16				
MM	309.9	63.4	3335	543
ME	72.3	21.9	698	227
ER	102.3	55.4	1150	611
RM	135.4	67.9	1470	639
EM	237.7	57.4	2629	512
LM[a]	83.7	27.1	803	292
LE[a]	150.9	22.9	1459	208
4. L, E, $\bar{l}$ = 103.1 ± 7.1 mm, n = 63				
MM	471.2	51.8	4672	526
ME	248.6	31.3	2297	317
ER	93.6	60.8	947	601
RM	128.5	68.5	1339	718
EM	222.0	52.9	2309	586
ML	121.6	28.5	985	295
LE	129.5	19.8	1312	218
LM	349.6	52.0	3609	591

[a] Interval begins prior to molt cycle in question.

short days at different times with respect to the time of M, where they remained for either 80 or 120 d (SDP) before being returned to a cool long-day system (L). No differences were found between 80- and 120-d SDP groups (Nelson et al. 1988a), and they are not differentiated in this report. To accelerate incubation and molting, females in the cool long-day system often were transferred to a warm long-day system, 172 ± 99 d post-L. Fifty-six percent of extruders and 11% of nonextruders were so treated. A nonextruding control group (none of whom extruded eggs during its previous molt cycle) was maintained on long-day photoperiod throughout a molt cycle. Forty-three percent were transferred from the colder to the warmer long-day system 167 ± 38 d postmolt to discover the effects of small temperature changes. Analysis of the relationships between intermolt interval I_{MM} and size and temperature (Appendix 1) suggested expressing intervals both in days (d) and as the sum of day-degrees above 6°C (dd$_6$), the latter to incorporate the effect of varying temperature in phase comparisons (Table 2).

Four years of experimental data from an average of 2.30 ± 0.77 completed molt cycles per female form the basis for the present report. Independence of successive molt cycles from the same female was assumed, for reasons outlined in Nelson et al. 1988a. M–L intervals (D_{ML}, Table 1) were approximately normally distributed with a mean of 1112 ± 446 dd$_6$; 70% of L values were between 600 and 1400 dd$_6$ postmolt, and 14% were between 1400 and 600 dd$_6$ prior to the next M. No transfer from short to long days occurred within ±200 dd$_6$ of M, nor from long to short days while a female was ovigerous (and typically resident in the nursery system until after hatching).

Experimental Groups, Terminology, and Statistical Treatment

In this way were generated four groups of *molt cycles*, distinguished by the presence or absence of E on the one hand and the presence or absence and timing of L on the other (Table 1C):

Group 1. NoL, NoE; n = 28, control group. None of these molt cycles contained either an L or an E, nor were any preceded or immediately followed by E.

Group 2. L, NoE; n = 75. Molt cycles in this group contained an L, but evidently the M–L interval was too long ($\bar{D}_{ML}$ = 1214 ± 326 dd$_6$, Table 2) to be compatible with immediate extrusion (Nelson et al. 1988a). Thirty-two of these were preceded by E in the previous cycle, and 11 (those with L sufficiently close to the following M; Nelson et al. 1988a; L–M interval $\bar{D}_{LM}$ = 803 ± 292 dd$_6$) were followed by immediate E in a molt cycle of the next category.

Group 3. NoL, E; n = 19. Extrusion occurs soon after the initial M, without an intervening L, the latter having occurred near the end of the previous molt cycle. Eight of the preceding molt cycles contained an E.

Group 4. L, E; n = 85. Molt cycles containing an E delayed by an L occurring relatively soon after the initial M (Nelson et al. 1988a; M–L interval $\bar{D}_{ML}$ = 985 ± 295 dd$_6$). Twenty-eight of these were preceded by E in the previous cycle.

Where molt cycles preceded or immediately followed by E must be distinguished, the group designations are followed

TABLE 3. Multiple regressions of interval duration I in days upon carapace length l in mm and temperature (measured as $S = T^{-1}$ in °C^{-1}, and regression of interval duration D in dd$_6$ upon l. Std. = standardized regression coefficient, a measure of partial correlation; r = correlation coefficient, M = molt, L = long day onset, E = extrusion. Groups are classified according to presence or absence of L and E during molt cycle. In the absence of extrusion (Groups 1 and 2), intervals are significantly positively correlated with l but not with S; when an extrusion is present the correlation with l is absent or even negative.

	I (d)							D (dd$_6$)			
		l			S				l		
Group	Intercept	Coef.	Std.	p	Coef.	Std.	p	Intercept	Coef.	r	p
1. NoL, NoE											
MM	−395.5	6.74	0.466	0.019	525	0.058	>0.5	−4456	78.2	0.494	0.009
2. L, NoE											
MM	23.8	2.99	0.287	0.067	67.5	0.006	>0.5	−1811	49.4	0.463	0.000
LM	−335.7	4.82	0.427	0.004	456	0.051	>0.5	−3622	55.1	0.478	0.000
3. NoL, E											
MM	−23.86	0.593	0.081	>0.5	2944	0.563	0.037	3087	2.45	0.039	>0.5
ME	153.5	−1.019	−0.403	>0.1	207	0.138	>0.5	2012	−12.9	−0.486	0.025
EM	−145.2	1.924	0.290	>0.1	2086	0.463	0.068	917	17.0	0.287	>0.1
LE[a]	37.59	−0.094	−0.151	>0.1	1190	0.461	0.069	1467	0.10	0.003	>0.5
4. L, E											
MM	526.0	−2.009	−0.277	0.027	1508	0.161	>0.1	6521	−17.9	−0.244	0.050
ME	104.3	−0.962	−0.217	0.044	2282	0.531	0.000	3339	−10.1	−0.227	0.039
EM	202.6	−0.562	−0.075	>0.5	811	0.129	>0.1	3086	−7.53	−0.092	>0.1
LE	37.13	0.357	0.129	>0.1	556	0.311	0.007	499	7.80	0.261	0.016
LM[a]	402.9	−0.289	−0.040	>0.5	242	−0.027	>0.5	3832	−2.17	−0.026	>0.5

[a] Interval begins prior to molt cycle in question.

TABLE 4. Differences between long day onset – extrusion groups in intermolt interval I_{MM} by ANCOVA with carapace length l and inverse temperature S_{MM} as covariates (above diagonal), and differences between slopes of the regressions of I_{MM} on l and S_{MM} (below diagonal). L = long day onset; E = extrusion, M = molt, R = egg release.

	1. NoL, NoE	2. L, NoE	3. NoL, E	4. L, E
1. NoL, NoE		$F = 0.39$ df 1,79 $p > 0.5$	$F = 0.26$ df 1,40 $p > 0.5$	$F = 8.9$ df 1,81 $p < 10^{-4}$
2. L, NoE	$F = 0.64$ df 2,77 $p > 0.5$		$F = 0.70$ df 1,67 $p > 0.4$	$F = 110.6$[a] df 1,113 $p < 10^{-4}$
3. NoL, E	$F = 2.93$ df 2,38 $p = 0.066$	$F = 1.96$ df 2,65 $p = 0.149$		$F = 92.7$[b] df 1,74 $p < 10^{-4}$
4. L, E	$F = 5.25$ df 2,79 $p = 0.008$	$F = 4.26$[a] df 3,110 $p = 0.007$	$F = 0.85$[b] df 3,71 $p > 0.4$	

[a] D_{ML} (M–L interval in dd$_6$) added as covariate to correct for minor experimental differences between groups.

[b] D_{ER} (E–R interval in dd$_6$) added as covariate to correct for minor experimental differences between groups.

respectively by EPREV or EFOL (Table 1). Where molt cycles differing in duration of egg or embryo retention interval are compared, the group designations are followed by SLOUGH ($D_{ER} \leq 1000$ dd$_6$) or HATCH ($D_{ER} > 1000$ dd$_6$).

The variables of interest in this report are summarized in Table 1D and 1E. They include *molt increment* G_M, the difference in carapace length l before and after the molt (measured in the hard shell condition), and the *durations of intervals* between events of four classes: molt (M), long day onset (L), extrusion (E), and egg hatching or other loss (R). Interval durations are given either as I in days (d) or as D in day-degrees above 6°C (dd$_6$; see Appendix 1 for explanation) or in both.

In addition, the ratio S between an interval I (measured in days) and the same interval D (measured in dd$_6$) ($S = I/D = T^{-1}$°C^{-1}, the reciprocal of average temperature above 6°C) was used as a covariate representing "inverse temperature" in multiple regressions of interval durations. This measure rather than its reciprocal was used because of its usually positive and more

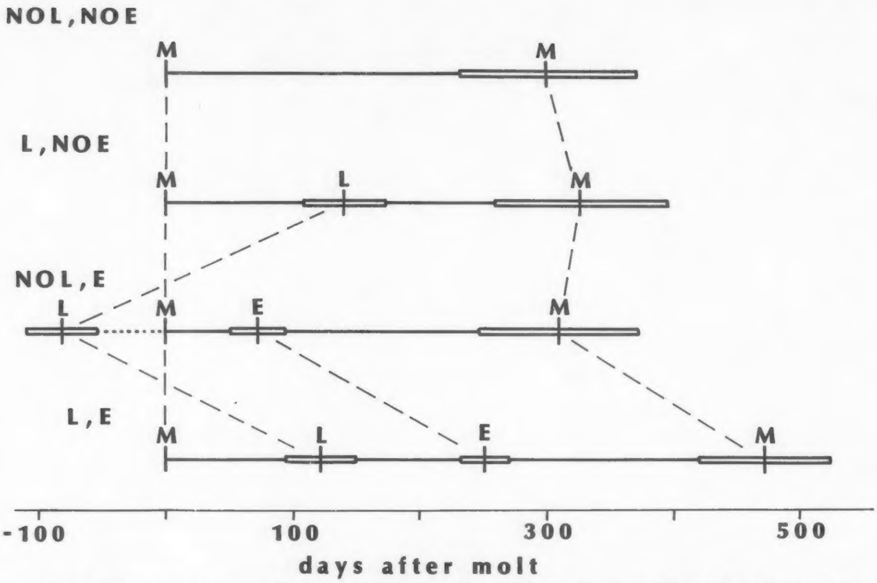

FIG. 1. When long day onset (L) is delayed beyond the molt (M), extrusion (E) and the following M are delayed. Average interval durations in days for four groups of molt cycles. Letters mark durations from initial molt to event identified. Open error bars mark standard deviations of those intervals, except for Group L, E (bottom line) where the error bar about "E" signifies the standard deviation of the L–E interval (I_{LE}).

TABLE 5. Mean and standard deviation of interval duration in dd_6 for molt–molt intervals (D_{MM}) and extrusion–molt intervals (D_{EM}) in different subgroups of extrusion-containing molt cycles (number of molt cycles in parentheses). M = molt, L = long day onset, E = extrusion, R = egg release, EPREV, NoEPREV = E present or absent in preceding molt cycle, SLOUGH, HATCH = E–R interval less than or greater than 1000 dd_6. NoEPREV and HATCH (and NoL, E and HATCH) appear to increase D_{EM} in an additive fashion.

	SLOUGH		HATCH	
Group	D_{MM}	D_{EM}	D_{MM}	D_{EM}
3. NoL, E	3122±500 (7)	2449±362 (7)	3500±543 (9)	2769±585 (9)
4. L, E				
EPREV	4346±275 (8)	1900±441 (8)	4700±518 (8)	2303±730 (8)
NoEPREV	4529±533 (21)	2207±507 (21)	4879±516 (26)	2562±526 (26)

significant linear correlations with interval duration in days (Table 3). We were thereby enabled to use linear regression with some justice throughout the interval analysis; cumulative normal probability plots of interval distributions were also usually more linear (thus, their distributions were more normal) than either their logged or their reciprocal equivalents.

Within a category of molt cycle, interval data were analyzed by multiple linear regression of interval length I upon carapace length l and inverse temperature S and linear regression of interval length D upon l (Table 3). To adjust for minor random differences between experimental groups, other interval durations in dd_6 were sometimes added to the regression equation. Comparisons of interval durations for molt cycles belonging to different groups or subgroups were by analysis of covariance (ANCOVA) with l, S, and sometimes duration of other intervals as covariates, again to adjust for minor differences between groups. Equality of slopes of the corresponding regression equations for the groups being compared was tested at the same time.

Three measures of growth were employed: molt increment G_M, growth rate $G_{MM} = 365G_M/I_{MM}$, and instantaneous growth rate G according to the Pütter (1920) model for increase in length: $G = dl/dt = E - kl$. For each molt cycle, G was estimated as $kG_M/(1 - \exp(-kI_{MM}/365))$ (for a more detailed explanation, see Appendix 2). k was approximated by iteration of the least-squares regression $G = a - kl + bT_{MM}$, where $T_{MM} = S_{MM}^{-1}$, the average temperature above 6°C. As with the interval measures, the relationships of growth measures within and among groups were analyzed by multiple linear regression and ANCOVA, but T_{MM} was used as a covariate, as there was no theoretical or practical justification for employing its reciprocal.

Results

Duration of Molt Cycle

Means and standard deviations of carapace length l and interval durations I and D are given in Table 2. The mean M–M interval durations I_{MM} for Groups 1, 2, and 3 (respectively NoL, NoE; L, NoE; and NoL, E) are similar; that for Group 4 (L, E) is much longer (Table 4, above the diagonal; Fig. 1). Evidently, neither an L by itself (Group 2, L, NoE) nor E by itself (Group 3, NoL, E) within a molt cycle is sufficient to prolong it. But if a delayed L does result in E (Group 4, L, E), that E is delayed and in turn occasions a delay of the following

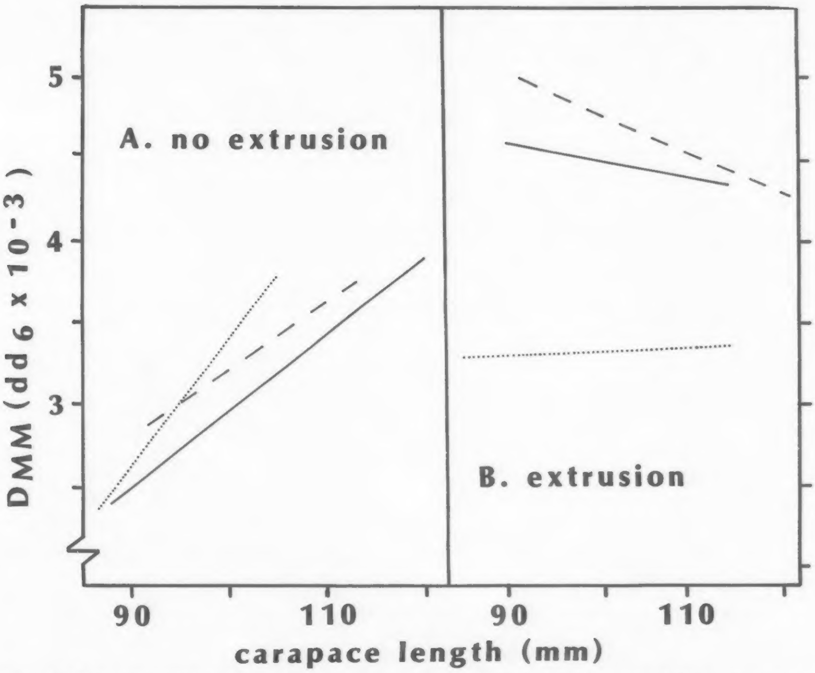

FIG. 2. When an extrusion (E) occurs, the intermolt interval loses its positive correlation with carapace length l. Duration of intermolt interval in day degrees above 6°C (D_{MM}) as a function of carapace length l. Dotted lines = molt cycles not containing long day onset (L), (A) with no E (group NoL, NoE), and (B) with E (group NoL, E). Solid and broken lines = molt cycles containing L, respectively with and without E (EPREV and NoEPREV) in previous molt cycle. In Fig. 2A, the subgroups represented are L, NoE, NoEPREV (broken line) and L, NoE, EPREV (solid line). In Fig. 2B, the subgroups represented are L, E, NoEPREV (broken line) and L, E EPREV (solid line). Projection of the regression line on the abscissa gives the range over which it was estimated. Regressions were corrected for minor differences between subgroups in D_{ML} and D_{ER} where applicable.

M (Group 4, L, E, $D_{ME} = 1330 + 0.803D_{ML}$; $r = +0.69$, $p < 10^{-4}$; all extrusions, $D_{MM} = 2925 + 0.736D_{ME}$; $r = +0.70$, $p < 10^{-4}$).

That the difference in M–M interval between NoL, E and L, E molt cycles lies in the delay of E by delayed L and not in another aspect of the situation may be seen by comparing the E–M intervals (I_{EM}, D_{EM}, Table 2; see also Table 5). These are actually longer although not significantly so in NoL, E than in L, E molt cycles (ANCOVA of I_{EM} regressed upon l, S_{EM}, and D_{ER} to correct for small differences between experimental groups, $F = 2.03$, df 4,74, $p > 0.1$).

Dependence of Interval Duration upon Size and Temperature

In Table 3, interval duration in days for those intervals not directly affected by the experimenter or the clutch is regressed linearly (*pace* Mauchline 1977) upon carapace length l and inverse temperature S. It is evident that for those molt cycles not including E (NoL, NoE and L, NoE) that I_{MM} is positively correlated with l and shows little correlation with temperature. In contrast, with molt cycles containing an extrusion, I_{MM} is insignificantly or even negatively correlated with l, but shows higher correlations with S_{MM}. (We had earlier and erroneously concluded that NoL, E molt cycle duration was positively correlated with l; Nelson 1986, fig. 6).

In Table 4, differences between L, E groups in slope of the multiple regression of I_{MM} upon l and S_{MM} are expressed below the diagonal by the corresponding F-ratios. Presence of L in a molt cycle does not affect the slope of the regression significantly; presence of E results in a larger (although not always significant) F-ratio.

With molt cycles lacking E, the significance of the correlations of interval durations with l is greatly increased when the former are expressed in terms of dd_6; this is not evident for molt cycles with E (Table 3; see also Appendix 1 for a related discussion). This furthers the impression that when E supervenes, factors other than female size become the major determinants of molt cycle duration.

Dependence upon Prior Extrusion

In Fig. 2, the regressions of D_{MM} upon l for the four L, E groups are plotted. For Groups 2 and 4, containing L, there are sufficient data to subdivide each group into those in which the preceding molt cycle contained or did not contain E (EPREV vs. NoEPREV). Molt cycles that follow a prior E (EPREV) are shorter than those that do not, whether or not the current one contains an E (L, E, NoEPREV vs. EPREV, with l, S_{MM}, D_{ML}, and D_{ER} as covariates to adjust for minor experimental differences, adjusted $\bar{I}_{MM} = 479.5$ vs. 446.9 d, $F = 5.25$, df 1,57, $p = 0.026$; the difference is greater without the adjustment for D_{ML}; L, NoE, NoEPREV vs. EPREV, with l, S_{MM}, and D_{ML} as covariates, adjusted $\bar{I}_{MM} = 346.6$ vs. 318.0 d, $F = 4.08$, df 1,52, $p = 0.049$).

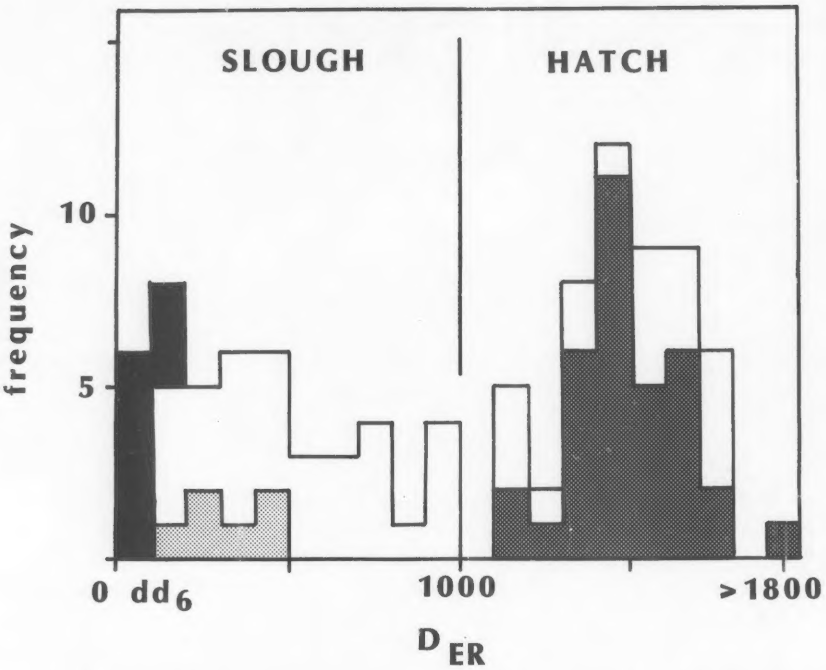

FIG. 3. Histogram of egg (or embryo) retention interval D_{ER}) in day degrees above 6°C (dd$_6$). Black = clutch stripped within 180 dd$_6$ of discovery of extrusion; light stippling = "backcross" clutches from attempted matings with sterile hybrid males; dark stippling = clutches known to have hatched at least some larvae. SLOUGH and HATCH categories are defined on the basis of D_{ER}, respectively less or greater than 1000 dd$_6$.

TABLE 6. Three measures of growth rate. Means and standard deviations for carapace length increment at molt (G_M) and growth rate ($G_{MM} = 365\ G_M/I_{MM}$; $G = dl/dt$). Means in parentheses adjusted to l = 100 mm and T_{MM} = 10 ($\bar{t}$ = 16°C) by the regressions in Table 7. L = long day onset, M = molt; E = extrusion, EFOL, NoEFOL = L, NoE molt cycles followed or not followed by NoL, E molt cycles. Presence of L in a molt cycle and presence of E either in the current molt cycle or soon after the molt are each associated with a decrement in growth for the current molt cycle.

	G_M (mm)		G_{MM} (mm·yr^{-1})		G (mm·yr^{-1})	
Group	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1. NoL, NoE n = 24	7.24 (7.26)	2.04	9.02 (8.36)	3.14	9.47 (8.83)	3.24
2. L, NoE						
a. NoEFOL n = 48	5.66 (5.24)	2.02	6.28 (5.79)	2.41	6.52 (6.11)	2.49
b. EFOL n = 7	4.37 (4.86)	1.54	5.40 (5.07)	1.35	5.54 (5.26)	1.36
3. NoL, E n = 11	3.71 (4.54)	1.23	4.42 (4.85)	1.02	4.58 (5.08)	1.07
4. L, E n = 33	4.64 (4.47)	2.10	3.65 (3.54)	1.53	3.75 (3.65)	1.60

The EPREV-NoEPREV difference similarly averages about 30 d (adjusted) with or without a current E. There is a suggestion that the difference is similarly larger with smaller females (Fig. 2; in neither case are the within-group regression slopes significantly different, however). At first this apparent relationship with size seems to be complementary to the difference in *current* molt cycle duration between Group L, E and the other groups (Tables 2, 3, 4; Figs. 1, 2) such that if the preceding molt cycle was prolonged, the current one is compensatorily abbreviated. However, in contrast with that relationship, molt cycles following prior E are shorter whether or not the prior E was delayed. The adjusted I_{MM} means in both Groups L, NoE

TABLE 7. Multiple regressions of growth measures upon size l, mean temperature above 6°C (T_{MM}), and (for G_M only) intermolt interval I_{MM}. G_M = molt increment, $G_{MM} = 365G_M/I_{MM}$, $G = dl/dt$, Std. = standardized regression coefficient, L = long day onset, M = molt, E = extrusion, EFOL, NoEFOL = L, NoE molt cycles followed or not by NoL, E molt cycles. l and T_{MM} coefficients are almost uniformly negative; intercepts and I_{MM} coefficients are uniformly positive.

			l			T_{MM}			I_{MM}		
Group	Variate	Intercept	Coef.	Std.	p	Coef.	Std.	p	Coef. ($\times 10^{-2}$)	Std.	p
1. NoL, NoE	G_M	7.45	0.0126	0.029	>0.9	−0.312	−0.122	>0.5	0.561	0.198	>0.4
	G_{MM}	25.68	−0.1254	−0.185	>0.4	−0.478	−0.121	>0.5			
	G	26.03	−0.1226	−0.175	>0.4	−0.494	−0.122	>0.5			
2. L, NoE											
a. NoEFOL	G_M	13.37	−0.0647	−0.208	>0.2	−0.397	−0.119	>0.4	0.707	0.258	0.099
	G_{MM}	20.13	−0.0826	−0.221	>0.1	−0.608	−0.152	>0.3			
	G	20.67	−0.0834	−0.219	>0.1	−0.622	−0.151	>0.3			
b. EFOL	G_M	11.25	−0.0608	−0.261	>0.5	−0.646	−0.283	>0.5	1.769	1.217	0.103
	G_{MM}	16.90	−0.0617	−0.303	>0.5	−0.562	−0.282	>0.5			
	G	16.62	−0.0604	−0.294	>0.5	−0.532	−0.264	>0.6			
3. NoL, E	G_M	9.84	−0.0649	−0.476	0.077	−0.296	−0.339	>0.3	1.203	0.645	0.063
	G_{MM}	17.54	−0.0838	−0.734	0.045	−0.428	−0.583	0.096			
	G	18.41	−0.0872	−0.731	0.045	−0.461	−0.602	0.086			
4. L, E	G_M	7.74	−0.0391	−0.117	>0.5	−0.720	−0.183	>0.2	1.713	0.329	0.092
	G_{MM}	13.97	−0.0418	−0.170	>0.3	−0.623	−0.216	>0.2			
	G	14.50	−0.0438	−0.173	>0.3	−0.647	−0.217	>0.2			

TABLE 8. Differences between groups in molt increment G_M (above diagonal) and growth rate G_{MM} (below diagonal), by ANCOVA with length l, temperature T_{MM}, and (for G_M) intermolt interval I_{MM} as covariates. L = long day onset, M = molt, E = extrusion, EFOL, NoEFOL = L, NoE molt cycles followed or not by NoL, E molt cycles. Significant differences ($p < 0.05$) in G_{MM} all involve either the fastest growing NoL, NoE group or the slowest growing L, E group, or both.

Group	NoL, NoE	NoEFOL	EFOL	NoL, E	L, E
1. NoL, NoE		$F = 7.62$ df 1,68 $p = 0.009$	$F = 10.62$ df 1,27 $p = 0.003$	$F = 13.31$ df 1,31 $p = 0.001$	$F = 13.8$ df 1,53 $p = 0.0005$
2. L, NoE					
a. NoEFOL	$F = 11.5$ df 1,68 $p = 0.001$		$F = 6.05$ df 1,12[a] $p = 0.030$	$F = 1.52$ df 1,55 $p > 0.3$	$F = 1.65$ df 1,77 $p > 0.2$
b. EFOL	$F = 5.75$ df 1,27 $p = 0.024$	$F = 4.06$ df 1,12[a] $p = 0.066$		$F = 0.07$ df 1,14 $p > 0.7$	$F = 0.30$ df 1,77 $p > 0.5$
3. NoL, E	$F = 9.00$ df 1,31 $p = 0.005$	$F = 0.79$ df 1,55 $p > 0.3$	$F = 0.22$ df 1,14 $p > 0.6$		$F = 0.38$ df 1,40 $p > 0.5$
4. L, E	$F = 48.9$ df 1,53 $p < 10^{-5}$	$F = 18.2$ df 1,77 $p < 10^{-4}$	$F = 5.77$ df 1,36 $p = 0.022$	$F = 4.50$ df 1,40 $p = 0.04$	

[a] Includes L, NoE, NoEFOL molt cycles with L–M interval $I_{LM} \leq 140$ d only, to be more comparable with EFOL group.

and L, E are in fact slightly larger with delayed than with undelayed prior E. Furthermore, there is no negative correlation demonstrable between current D_{MM} and preceding I_{MM} (temperature records for preceding I_{MM} values incomplete; L, E, NoEPREV: $r = 0.000$, $n = 38$; L, E, EPREV: $r = +0.114$, $n = 13$; with other subgroups the correlation is even more positive, because of the positive correlation of both preceding and following interval with size). The effect is similar whether the prior extrusion was SLOUGH or HATCH (Table 1): E and not embryo retention appeared to be the operative factor.

Effect of Presence of Clutch

The bimodal distribution of embryo retention interval D_{ER} (Fig. 3) suggested dividing it into two categories, SLOUGH and HATCH, at D_{ER} = 1000 dd_6 (the composition of these categories is discussed in detail in Appendix 3).

D_{EM} and D_{MM} durations for molt cycles containing SLOUGHed extrusions were approximately 350 dd_6 shorter than those in the HATCH category, in all L, E subgroups (Table 5). This strongly suggested that presence of the clutch on the pleopods increased the duration of the molt cycle, inde-

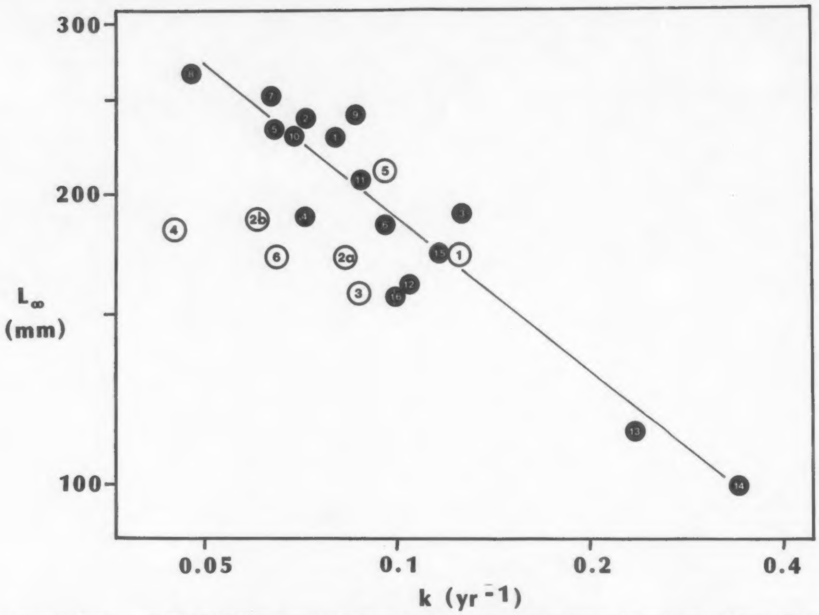

FIG. 4. Pütter – von Bertalanffy parameters for selected lobster populations and conditions. Open circles represent laboratory studies: Groups of adult females from the present study (Table 6) were (1) NoL, NoE, (2a) L, NoE, NOEFOL, (2b) L, NoE, EFOL, (3) NoL, E, (4) L, E, (5) male Rhode Island lobsters reared at Wickford (Hadley 1906) (parameters calculated by Pütter 1920), and (6) European lobsters (*Homarus gammarus*) reared by Hewett (1974). Solid circles represent field studies: Groups 1–9 compiled by Russell (1980); (1 and 2) offshore populations, southern New England, females, (3–9) inshore northeastern United States samples, from southwest to northeast: New Jersey, Western Long Island Sound, Connecticut, Rhode Island females, Massachusetts, and two studies from Maine, (10 and 11) Bay of Fundy females, parameters estimated by two methods (Campbell 1983), (12) Nova Scotia females (Gabarus Bay, data of Wilder, reported by Robinson 1979), (13 and 14) Newfoundland females, two localities: Placentia Bay (Ennis 1980) and Comfort Cove (Ennis et al. 1982), (15 and 16) European populations: Ireland (Gibson 1967) and Norway, females (Conan and Gundersen 1979). The solid line is the power function fitted to the *Homarus americanus* inshore population points 3–14: $L_\infty = 55.75k^{-0.53}$, $r^2 = 0.898$. An anonymous reviewer suggested that this regression may be related to the principal axis of the joint confidence ellipse of k and L_∞ (which would have a similar slope if L_∞ is approximately double the mean l in the sample).

pendently of delay of molt by L-delayed E or of advance by prior E. However, shorter molt cycles might be associated with ovarian incompetence (see Appendix 3), and experimental test was desirable.

D_{EM} durations associated with unfertilized and sloughed "backcross" extrusions (Fig. 3) following mating to hybrid males (*H. americanus* × *H. gammarus*) were an average of 520 dd_6 shorter than those following comparable homotypic extrusions with which they were paired ($t = -3.02$, df 4, $p < .025$, one-tailed), and thus, presence of an empty spermatophore was insufficient to delay M. It still remained possible that presence of *viable* sperm in the spermatophore was requisite both to successful ovulation and to M delay more directly. To exclude such a possibility, one member of a carefully matched pair was stripped of its clutch, as described under Materials and Methods. D_{EM} was an average of 341 dd_6 shorter in the stripped members of pairs ($t = 1.95$, df 7, $p < 0.05$, one-tailed). This directly indicated that presence of embryos on the pleopods can result in delay of the ensuing M.

Even among the HATCH group, however, the interval between hatching and the following molt (D_{RM}) was both large and highly variable. This variation is to be contrasted with that of the immediately preceding incubation period (D_{ER} vs. D_{RM}, for all HATCH, EPREV molt cycles: $\bar{x} = 1494 \pm 115$ dd_6 vs. 929 ± 649 dd_6; for all HATCH, NoEPREV molt cycles: $\bar{x} = 1502 \pm 236$ dd_6 vs. 1053 ± 587 dd_6). Reflecting this R–M variability, in the present experiment, four clutches were lost through molting (i.e. $D_{RM} = 0$) (see also Aiken 1980). Although all four belonged to the HATCH category by the time of M, none was associated with particularly long D_{ER}, only one with a particularly long D_{ME}, and two with a prior E; for three, l was less than 100 mm. Furthermore, between SLOUGH and HATCH categories, 1100 dd_6 of additional incubation results in little more than 350 additional dd_6 of molt cycle duration.

Effects upon Molt Increment and Growth Rate

To discuss the effects of photoperiod and extrusion on carapace length increment (G_M) at the molt terminating the molt cycle, we must recognize subgroups of the L, NoE group of barren molt cycles, according to whether (EFOL) or not (NoEFOL) they are followed by a molt cycle belonging to group NoL, E (Tables 6–8), that is whether they are associated or not with an immediately following extrusion E. EFOL and

NoEFOL molt cycles do not differ in I_{MM} or D_{MM} duration and are therefore grouped together in the analyses of Tables 2–4. But they do differ significantly in G_M, even when the comparison is restricted to NoEFOL molt cycles in which $I_{LM} \leq 140$ d, the maximum I_{LM} duration within the EFOL group (Table 8, above the diagonal).

Beyond that, all other significant differences in G_M are in comparisons involving the NoL, NoE group (Table 8, top row). Continuous long-day (and barren) molt cycles are terminated by molt increments that are larger than those ending barren molt cycles containing an SDP, and, perhaps surprisingly, these latter are not significantly larger than those molt increments which follow extrusions.

G_M terminating a molt cycle that is preceded by an E (EPREV) is hardly larger than G_M following one which is not ($F = 0.027$, $p > 0.8$). G_M following a SLOUGH extrusion is not significantly larger than that following a HATCH molt cycle ($F = 0.94$, $p > 0.3$).

Differences between groups in growth rate $G_{MM} = 365G_M/I_{MM}$ (Table 6) are significant when they involve either Group 1 (NoL, NoE) or Group 4 (L, E) or both, but not otherwise (Table 8, below the diagonal). G_{MM} during a molt cycle preceded by E is slightly larger than that for one which is not ($F = 0.90, p > 0.3$). G_{MM} during a SLOUGH molt cycle is, again, not significantly larger than that for a HATCH molt cycle ($F = 1.89, p > 0.1$).

In Table 7 are given the multiple regressions of G_M upon l, T_{MM} ($= S_{MM}{}^{-1}$), and I_{MM} and of G_{MM} upon l and T_{MM}. Several points deserve comment. First, G_M in uniformly negatively correlated with average temperature during the preceding molt cycle; although for no single regression is the coefficient significantly different from zero, the effect is consistent and the sensitivity pronounced. Second, G_M is uniformly positively correlated with I_{MM}, independently of its correlation with T_{MM}; i.e. within a molt cycle group, the longer the molt–molt interval, the larger the molt increment following it. Third, although the effect of size (l) upon G_M is not as uniform, when the measures of interval and increment are combined into the single growth rate measure G_{MM}, the effects of l upon that measure are again uniformly negative. Fourth, the coefficients relating G_{MM} to T_{MM} are uniformly negative, with only a small amount of variation between groups. Thus, there were no significant differences between groups in the slopes of the regressions of G_M upon l, T_{MM}, and I_{MM}, or in those of G_{MM} upon l and T_{MM}. The largest F-ratio among all such slope comparisons was 1.2.

Included also in Table 7 are estimated regressions upon l and T_{MM} for instantaneous growth rate G assuming growth to proceed according to the Pütter (1920) growth equation, also known as the von Bertalanffy growth equation (Ricker 1979: "Pütter growth curve No. 1"):

$$(1)\quad \frac{dl}{dt} = E - kl = k(L_\infty - l)$$

where $E = kL_\infty$ is a parameter representing both "anabolism" and initial growth rate, k represents both a "catabolism" constant and the rate of decline in growth rate with length, and L_∞ is asymptotic carapace length. For each molt cycle in a group, G is estimated by the method given in Appendix 2.

For each group in our experiment, values of k and L_∞ (from the regressions of Table 7, standardized to $T_{MM} = 10$, i.e. 16°C) are compared in Fig. 4 with values drawn from the *Homarus* literature.

Discussion

Our results concern, first, the effects of extrusion in prolonging the molt cycle and in removing the dependence of intermolt duration upon size; second, the modification of these effects by prior extrusion and the clutch; and third, the effects of secondary vitellogenesis and of extrusion upon growth rate, as functions of size and temperature. We discuss the implications of these results in turn. We will propose that molting and growth in the adult female lobster are separable processes that should be kept conceptually distinct.

Effects of Extrusion and of Its Delay

The present study compares four groups of molt cycles, characterized by presence or absence of a short day period and long day onset (L) and by presence or absence of extrusion (E) during the course of the cycle. Only if L falls within the postmolt period of extrusion potential (i.e. L is delayed with respect to M) does the ensuing delayed E occasion a significant delay of the following M (Table 4; Fig. 1).

But we find that intermolt interval, in Crustacea ordinarily an increasing function of body size (Hartnoll 1982), is independent of or even negatively correlated with carapace length l if the interval contains an E, whether delayed or undelayed (Table 3; Fig. 2) (Nelson (1986) erroneously concluded that I_{MM} for NoL, E molt cycles was positively correlated with l). Upon E, the "somatic," body-size-dependent control over the molt cycle is superceded by a size-independent "reproductive" program of control. The *delay* in M occasioned by E is therefore a decreasing function of size, even when extrusion itself is undelayed. Others (e.g. Lawlor 1976 in the isopod *Armadillidium vulgare*) have noted that the difference in duration between ovigerous and nonovigerous molt cycles in brooding malacostracans was particularly pronounced in smaller females. But in another isopod, *Porcellio dilatatus*, parturial molt cycle duration was found to remain an increasing function of size (Mocquard et al. 1976).

Final maturation of the oocytes, ovulation, or initial attachment of eggs to the pleopods rather than extrusion per se may well be the trigger of the reproductive program. Removal of eggs soon after attachment shortens but does not abolish the reproductive program (Table 5). Secondary vitellogenesis or other prior events associated with it such as proliferation in the cement glands of the pleopods (Aiken and Waddy 1982) may be essential for the establishment of the reproductive program but do not appear to be sufficient. When a too-long-delayed L fails to elicit a subsequent E (L, NoE molt cycle), it nevertheless may be followed by an immediate increase in cement gland stage (although not to as high an average level as when E ensues; Nelson et al. 1988a) and by hemolymph titers of vitellogenins comparable with those found in vitellogeneses which do result in E (Nelson et al. 1988b). There is also an associated decrease in the subsequent molt increment and in the growth rate measured over such L, NoE molt cycles (Tables 6 and 8). However, notwithstanding that L is delayed, the subsequent M is not (Tables 2, 4; Fig. 1), and the somatic program of dependence of intermolt interval upon carapace length remains fully in force (Tables 3, 4; Fig. 2A).

The functional importance of the reproductive program surely lies in provision of sufficient time for development and hatching of the clutch, particularly in smaller females. It is the incubation period, not the size of the female, that now must dictate the duration of the molt cycle, lest the clutch be lost with the exuvia.

Effects of Prior Extrusion and of Egg Retention

An E in the previous molt cycle was associated with a reduction in duration of the current cycle (a) whether or not the current molt cycle contained E (Fig. 2), (b) whether or not the E and M of the previous cycle were delayed, and (c) whether or not the M terminating the current cycle is delayed by egg retention (Table 5).

From (a), we may infer that the effect of prior E is felt under both the somatic and the reproductive programs. From (b), we can infer that the effect of prior E is not an effect of *delayed* prior E, as is the delay in M immediately following such an E. Furthermore, the effect is seen in the E–M duration (point (c); Table 5). It is not, in other words, a simple compensatory reduction in molt cycle duration following a prolonged previous cycle. Nor is it a result of different M–L durations consequent upon a shorter postmolt period in which L may elicit an E following such a delayed M (Nelson et al. 1988a): intermolt interval and E–M intervals remain shorter following a prior E even when adjusted for different M–L interval durations. It is a genuine effect of prior E or some closely associated event.

E (Fig. 2), prior E (Fig. 2B), and prior delayed E (in its effect upon the period with extrusion potential following M; Nelson et al. 1988a) all appear to result in increased independence from size of female in the timing of important subsequent events, but only under the reproductive program. Under the somatic program, prior E increases the slope of the regression of intermolt duration upon carapace length (Fig. 2A). The system appears to operate in a somewhat ad hoc fashion to provide for successful reproduction even in the event of a "worst-case scenario": small female, prior delayed E, current delayed E. In the event of E, the M can be delayed; an M delayed by E is still followed by an adequate postmolt period with extrusion potential; following a prior E and a delayed current one, there is almost always still time for even a small female to complete incubation (see also the final section of this discussion).

Stimuli from the embryos provide an additional margin of safety in all contingencies (Table 5). Aiken and Waddy (1976, 1980) and Aiken (1980) appear to have inferred from the occasional molted clutch in *Homarus* that premolt inhibition by the attached brood does not occur. We have demonstrated that retention of the clutch does prolong the molt cycle, but the effect is clearly not as direct as the inhibition of premolt by the expanded brood pouch in the isopod *Oniscus*, in which premolt begins within 3 d of its collapse (Steel 1980).

Dependence of molt delay in ovigerous females upon presence of brood has been demonstrated in several malacostracans (decapods, Hess 1941; Hiatt 1948; Scudamore 1948; Kurup and Adiyodi 1980; dependence upon expanded brood pouch in an isopod, Steel 1980). In the crab *Paratelphusia hydrodromous*, removal of the eyestalks removes this "brood effect" as well (Kurup and Adiyodi 1980).

In the decapod *Palaemon*, removal of the brood does not shorten the prolonged reproductive molt cycle (Kajishima 1949; Kamiguchi 1971a). Interestingly, neither does eyestalk removal. This led Kamiguchi (1971b) to suggest that inhibition of M following E may be under control of another endocrine organ, perhaps Passano's (1960) hypothetical analog of the corpora allata which produce juvenile hormone in insects. Blanchet-Tournier (1982) has postulated that in *Orchestia gammarella* the ovary during secondary vitellogenesis is capable of stimulating the production of molt-inhibiting hormone (MIH). Perhaps in decapods the ovary may manufacture its own molt-inhibiting principle. In *Homarus* and *Palaemon*, the occurrence of ovulation might stimulate the ovary to continue production of such a principle long after extrusion.

There is thus much suggestive evidence for a molt-inhibitory control specific to ovulatory molt cycles — the reproductive program — distinct from the size-dependent somatic control exercised during nonreproductive cycles by the eyestalk neurosecretory complex. But the additional effects of clutch retention and prior extrusion are more difficult to reconcile with this view. If the molt-inhibitory effect of the clutch is mediated via the eyestalk, as Kurup and Adiyodi (1980) seem to have shown in *Paratelphusia*, how is this effect communicated to the reproductive program, which appears to be independent of eyestalk control? Chang's (1984) evidence of a possible molt-inhibiting factor in an extract of fully developed pleopodal glands assayed upon eyestalkless juveniles seems only to complicate the picture. The fractional contribution by egg retention to M delay consequent upon E is not simply "added on" but seems rather to be integrated into the total delay, which is usually but not always sufficient to allow hatching.

Again, how is one to explain the effect of prior E upon both reproductive and somatic programs? Perhaps the effect of prior E is already felt at the beginning of the molt cycle, before the switch from somatic to reproductive control is made. But how is the reproductive program to be informed of this?

Effects of Reproduction upon Growth Rate

We found that both a period of short days (Groups L, NoE and L, E; Table 6) and an E during a molt cycle (Groups NoL, E and L, E) were associated with a reduction in molt increment and in growth rate. We will refer to such a reduction rather loosely as a "cost," without further explication.

It is doubtful that the cost incurred as a result of short days during a barren molt cycle (compare Groups NoL, NoE and L, NoE, NoEFOL; Table 6) is simply a result of slower somatic growth during those short days. We earlier found neither an increase in molt latency nor a decrease in molt increment in similarly sized adult females experiencing at least 100 more short days during barren molt cycles (8 h light : 16 h dark vs. 16 h light : 8 h dark, as in the present experiment; $\bar{G}_M = 8.33$ vs. 8.38 mm, $F = 0.004$; unpubl. results). Aiken and Waddy (1976) found a small effect of short day-length upon molt increment in juveniles, but they employed much more extreme photoperiod regimes (1 h light : 23 h dark vs. 20 h light : 4 h dark).

If the cost incurred as a result of a period of short days in a barren molt cycle (Group L, NoE) is not simply a result of slower somatic growth during short days, it may be rather a cost associated with the activation of reproductive processes: the cost of primary vitellogenesis during the SDP, and/or that of an abortive secondary vitellogenesis following L. In Appendix 3 and elsewhere (Nelson et al. 1988a) we have noted that the processes associated with secondary vitellogenesis are activated in barren cycles following a too-long-delayed L: increase in pleopod index and in size of ovary, in most cases higher hemolymph titers of vitellogenins. It is likely that these changes are paid for by a decreased G_M.

The highest costs appear to be borne by molt cycles with delayed E and M (L, E; Table 6). Why this should be so is unclear. There would seem to be more time in such a cycle over which to distribute the cost of reproduction than in a cycle with undelayed E (NoL, E). But we note that the L preceding such an undelayed E is in the previous cycle (Group L, NoE, EFOL; Table 6) and that the molt increment G_M is significantly smaller following such cycles than with similar cycles not followed by E (Group L, NoE, NoEFOL; Table 8). When L preceding M is followed by E in the next molt cycle, the cost of reproduction appears to be distributed between the two adjacent molt cycles. Otherwise, the cost incurred by E seems to be paid in full at the time of the following M; G_M is not reduced in the cycle following one with an extrusion.

It should be noticed that except for Group L, E, these costs are borne by the molt increment G_M and not by the molt interval I_{MM}. L, NoE cycles are no longer than NoL, NoE ones; EFOL cycles are no longer than NoEFOL ones; and on the average, NoL, E cycles are no longer than NoL, NoE ones. Furthermore, within each group, G_M is strongly dependent upon the intermolt interval (Table 7). Rate of molting ($1/I_{MM}$; Table 3) is uniformly a positive function of temperature and the growth measures are uniformly decreasing functions of temperature (Table 7).

We interpret these facts as meaning that the process, whether "somatic" or "reproductive," governing the duration of the adult female molt cycle is loosely associated with growth but sharply distinct from it. Growth *depends*, of course, upon molting, and the growth per molt upon the intermolt interval, but a lobster may, for example, molt without growing, for any of a number of reasons. As a crustacean grows and changes its reproductive status, the accompanying changes in molting frequency and growth rates are "separate but equal" processes of development (see also results of Vidal 1980). Botsford (1985) also came to the conclusion that molt increment and growth rate were the more appropriate measures of crustacean growth.

We find this independence surprising because in larval and juvenile lobsters the processes seem more tightly coupled. Growth rate differences resulting from differences in temperature, diet, and socially induced growth inhibition are most often expressed as differences in intermolt interval (Aiken 1980), molt increment being usually much more constant. For example, at moderate rearing temperatures, molt increment is nearly temperature independent in juveniles (Hughes et al. 1972; our unpubl. results) whereas it decreases with temperature in adults, as we have seen.

Figure 4 compares growth in our experiment with other estimates in terms of von Bertalanffy parameters L_∞ and k commonly found in fisheries investigations. We use the Pütter or special von Bertalanffy equation for increase in length as the simplest equation modelling a growth rate that declines with length (eq. (1)) and for its heuristic value: "growth" is what is left after "costs" are subtracted from "income," which does not grow with size as rapidly as do the costs. A modern discussion is found in Pauly (1979).

It is likely that with the small range of carapace lengths in our experiment, we have underestimated k and overestimated L_∞. Also, the positions of the points for Groups 2b (L, NoE, EFOL) and 4 (L, E) seem rather too far below the regression describing the field estimates. This is no doubt due to the higher average temperatures in our experiment. But in order to raise the L_∞ values for these groups to values on the regression line and to bring G_M values to those typical in the field, we need only extrapolate to temperatures 3–4° lower using the regressions of Table 6.

In fact, such extrapolations are probably not strictly legitimate. Aside from the fact that our regressions were obtained over very narrow temperature ranges (see Materials and Methods), we have included temperature as if it affected negatively the "anabolic" length-independent parameter of the Pütter equation (E in eq. (1)). In all likelihood, both E and the "catabolic" parameter k will *increase* with temperature, with k having the greater sensitivity to temperature change (e.g. Taylor 1958; Pauly 1979). Pütter (1920), in developing the implications of his equation, was the first to point this out (as well as the first to make an estimate of von Bertalanffy parameters for lobster growth, the open circle labelled "5" in Fig. 4). Taylor (1958) found in fitting von Bertalanffy parameters to growth data on cod (*Gadus callarias*) populations that the dependence of the parameters upon temperature was well described by power functions. The power of temperature for k was 1.643, about double that for his parameter i, closely related to E.

That k should be more sensitive to temperature than is E also helps us to visualize the difference in dependence of molt increment upon temperature between juvenile and adult lobsters. E dominates juvenile growth, the negative effect of k as a multiplier of l becoming important only with increasing size. If rate of molting ($1/I_{MM}$) is approximately linearly related to temperature above some threshold (see Appendix 1), it is easy to show that in terms of the Pütter equation (1), the condition for the growth increment in juveniles to be independent of temperature is that E also increase approximately linearly with temperature. The additional condition for adult molt increment to decline with temperature is that k increase with temperature faster than E, as we have just discussed.

Molting and Reproduction in the Natural Temperature Cycle

The implications of our results for the molting and reproductive cycles of female lobsters in the natural environment will be discussed in detail elsewhere. Here we briefly relate the events in the combined cycle to the temperature regime of southern Massachusetts coastal waters and draw a few conclusions. The mean yearly temperature cycle recorded by Hughes and Matthiessen (1962; updated version in Hughes et al. 1972) for Lagoon Pond, Martha's Vineyard, is nearly sinusoidal, with a mean annual temperature of approximately 13°C, peak and trough near August 10 and February 10, respectively, and peak-to-trough amplitude of approximately 20°. Thus, during the winter months the temperature falls below $\alpha = 6°C$ (see Appendix 1) for a time and a female may be unable to "accumulate" day-degrees. The mean annual temperature and peak-to-trough amplitude are probably several degrees higher here than in more open and deeper inshore areas (Davis 1978). Also, a reduction in peak-to-trough amplitude and a briefer or absent period of subthreshold temperatures will be experienced by a lobster that moves to deeper water in the winter (e.g. Stasko 1980).

The following observations assume a sinusoidal annual temperature cycle and our threshold-linear day-degree model of the effect of temperature upon physiological processes, but they should be valid with relaxation of these assumptions, for example with asymptotic approach to "physiological zero." We assume an annual mean temperature 2° lower than that of Lagoon Pond, the same peak-to-trough amplitude and phase relationships, an α of 6°C, and effective date of L near the vernal equinox (d080, March 21). A female with the mean characteristics of subgroup L, E. EPREV, HATCH (Table 5) should then extrude near mid-August (d222), carry eggs through the winter to hatch near mid-July of the following year (d190), and then molt in mid-September (d265). The scanty data for Massachusetts waters (chiefly Herrick 1896) suggest that our estimates are late for each date by at least several weeks. Advancing L by a few weeks or even months will not correct matters because L occurs during a period of below -6°C temperatures (December–April in this example); thus, we expect the exact timing of E and subsequent events to depend not upon the time of L, but upon the rapidity of vernal accumulation of day-degrees above threshold.

There are several possible reasons for this discrepancy. The day-degree metric or an α of 6°C may not be applicable to measuring the L–E interval, or extrapolation of this metric to near-threshold temperatures may not be justified. The average female may have spent the winter and early spring in deeper, warmer water, accumulating above-threshold day-degrees since the effective date of L, and hence completing vitellogenesis sooner.

That the *timing* of E in these circumstances would appear to depend less upon the date of L than upon the rate of the vernal onset of warmer temperatures leads naturally to the question, which cue is the effective *trigger* of vitellogenesis in the natural environment. We have repeatedly shown the necessity of a short-day period and the effectiveness of *L* as a trigger in our much more constant laboratory temperature regime (Nelson et al. 1983, 1988a; Nelson 1986). Preliminary results suggest that periods of 6°C of different durations terminating prior to or near L do not affect the L–E interval significantly (unpublished experiment with females from Massachusetts inshore and offshore populations). Finally, in the temperature regime experienced by offshore lobsters, there may be no vernal increase in temperature (see discussion in Nelson 1986), yet they appear also to extrude during July and August (unpublished analysis of mark–recapture data in Uzmann et al. 1977). Nevertheless, Aiken and Waddy (1985, 1986) have shown that in a more natural temperature regime, lobsters from Prince Edward Island are uninfluenced by photoperiod in the timing of their extrusions; however, they have not demonstrated that the trigger is increasing spring temperature. We must conclude that the question of which cue is actually operative in triggering vitellogenesis is still unresolved for all natural populations of American lobsters.

In our experiment we found that if L was delayed by more than 600 dd$_6$ after M, the probability of E rapidly fell (Nelson et al. 1988a). For our model female, L the following spring is less than 600 dd$_6$ after a mid-September M, so she should experience no difficulty in successfully producing a clutch of eggs. But if she had molted much earlier than late August, or if the mean temperature during the fall was much higher, her chances of extrusion might be seriously compromised. This result is again irrespective of the exact effective date of L, as long as this date falls during the hibernal period of below-threshold temperatures. An increase in annual mean temperature of 1° in our model advances E by 8–10 d and hatching and M each by 1 mo; at such an M, the next L is now as much as 1000 dd$_6$ away and the probability of a following E is reduced by half.

A decrease in annual mean temperature from 11 to 10°C delays extrusion by 7–9 d and hatching by a little less 1 mo; but it may result in our model in a delay of several months in the subsequent molt. With but a slightly lower autumnal temperature, that molt may be postponed until the following spring, possibly in turn delaying the next extrusion (Table 2, category 3, NoL, E). For such a female, the meshing of molting, growth, and reproduction, and in particular the phase of extrusion in the molt cycle, may be remarkably sensitive to relatively minor fluctuations in the annual cycle of temperature.

NOTE ADDED IN PROOF

Recent experiments by Waddy and Aiken (1987 and pers. comm.) have confirmed our suggestion (Nelson 1986; Nelson et al. 1988a) that the photoperiodic vitellogenic response in Prince Edward Island lobsters is indeed similar to that in Massachusetts inshore lobsters, but that it is overridden by temperature in the natural northern inshore environment.

Acknowledgements

We thank John Hughes, former Director of the Massachusetts State Lobster Hatchery, Vineyard Haven, for his cooperation in obtaining lobsters, and L. W. Botsford and E. S. Chang for their helpful comments on the manuscript. This project was supported by NOAA, National Sea Grant College Program, Department of Commerce, under project Nos. R/A45 and R/A65, through the California Sea Grant College Program. We thank C. J. Culp and D. Cosgrove for preparing the manuscript.

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Appendix 1. Estimating α

Although temperature variation in our experiment was not large, it was characterized by seasonal and other sources of serial correlation. Females molted at different times and perforce spent varying times in the warmer long-day system as a matter of practical necessity; hence their individual and group-average temperature records were somewhat different. It was thus essential first to find a common currency in which their molting and reproductive histories could be expressed, which would incorporate the variance due to temperature. It was necessary to use different approaches for the different groups in the study, but all methods led to the same day-degree metric.

The temperature dependence of development and growth has been expressed as an exponential, as a catenary, and as a power function of temperature (summarized in Ricker 1979). Usually it is necessary to specify a "zero" other than 0°C. For the catenary, this zero is the temperature of maximum growth rate, but otherwise, it is usual to think of it as some empirically determined "physiological zero" for the process involved. Thus we have the power function of Bělehrádek (1935):

$$\text{(A1)}\quad \begin{aligned} v &= A(t-\alpha)^B, & \alpha < t < t' \\ &= 0, & \alpha \geqslant t \end{aligned}$$

in which v, the rate of the process, is dependent upon the temperature above α, the "physiological zero," within a range with upper bound t'.

We surveyed four studies of *Homarus* development (Templeman 1936, 1940; Perkins 1972; Branford 1978). We found by an iterative procedure the value of α in each case that maximized the coefficient of determination r^2 as an estimator of the best fit to eq. (A1), allowing the other parameters to "float" (Branford (1978) had calculated A and α for *H. gammarus* incubation time but, following Wear (1974), had used an apparently arbitrary and erroneous value of $B = 2.3$). We obtained averages for α and B respectively of 4.64 ± 1.70°C and 1.062 ± 0.201.

Using a similar procedure for *H. americanus* juvenile growth rate, Rauch et al. (1974) estimated B as between 0.5 and 1.2 for α between 7.2 and 1.7°C, respectively. Small changes in either parameter gave similar results; with their data if B is 1.0 (i.e. the relationship threshold-linear), α is approximately 3°C. Aiken and Waddy (1976) suggested without presenting a detailed analysis that the molting frequency of older juvenile *H. americanus* is a linear function of temperature above a threshold of about 5°C.

Over the small range of temperatures represented in our experiment the assumption of linearity ($B = 1$) is thus well justified. We must further assume that temperature affects different stages of the molt cycle in a similar way, which also appears to be justified (Richard 1978). Interval durations may then be made to incorporate the effects of varying temperature by expressing them in "day-degrees" (Beck 1980: "thermal units"):

$$\text{(A2)}\quad D = \sum^{i} \delta\,(t_i - \alpha),\ \ \begin{aligned} &\delta = 0 \text{ for } t_i \leqslant \alpha \\ &\delta = 1 \text{ for } t_i > \alpha,\ i = 1,2,\ldots,I \end{aligned}$$

where D is the duration measured in day-degrees above α, t_i is the temperature in degrees Celsius recorded on the ith day, and I is the duration of the process in days. Robinson (1979) has suggested the appropriateness of day-degree reckoning in field studies of lobster molting patterns.

Molt–molt interval duration (I_{MM}) for the control group (Group 1, NoL, NoE), when regressed on carapace length l and the reciprocal of average temperature above 6°C, S_{MM}, shows a high partial correlation with l and a low, insignificant one with S_{MM} (Table 3). As a result from this least-squares regression, α would be grossly underestimated (see e.g. Ricker 1973) and would vary with l as well. We instead estimate α for this group as that value which when substituted in eq. (A2) would maximize the correlation coefficient r of the intermolt day-degree sum D_{MM} with l. The curve of r plotted against different values of α shows a single peak ($r = +0.494$) at approximately $\alpha = 6.5$°C.

In contrast, with Group 3 (NoL, E; Table 3), the partial correlation of I_{MM} with l was small and insignificant whereas that with S_{MM} was large and significant ($p = 0.037$). For this group we could estimate α directly from the x-intercept of the least-square regressions of $I_{MM}{}^{-1}$ upon average temperature as 5.4°C.

Unfortunately, neither procedure is valid for Groups 2 and 4 (L, NoE and L, E) because as we had previously demonstrated, inclusion in one or the other of these groups was based in part upon average temperature during the M–L interval (Nelson et al. 1988a). Each group represented a subset of molt cycles already selected in part by temperature; any least-squares or maximum likelihood estimation procedure would thus be misleading. Nor could the lumped set of molt cycles containing Ls (i.e. L, NoE + L, E) be used; the occurrence of extrusion completely alters not only average interval duration (Table 2) but also its relationship to both size and temperature (Table 3). However, we could estimate the value of α that minimized the variance in cutoff of M–L interval (D_{ML}) compatible with extrusion, or equivalently that maximized the difference between the M–L distributions (D_{ML}) from Groups 2 and 4, as between 6 and 7°C (Nelson et al. 1988a).

The estimates converge at approximately 6°C, and accordingly we choose this value for our day-degree metric. In Table 3, measuring intervals in dd_6 increases the correlations of interval lengths with l in Group 1 (by design) and also in Group 2, in both of which they are already large and positive, but does not particularly increase it in Groups 3 and 4, in which the dependence upon l by and large is small or even significantly negative.

Appendix 2. Estimating G, k, and L_∞

The parameters L_∞ and k of the Pütter (1920) or special von Bertalanffy growth equation (eq. (1), text) are usually estimated by fitting its integral form to length-at-age data by one of a number of methods (Ricker 1979):

$$\text{(A3)}\quad l_t = L_\infty\,(1 - e^{-k(t-t_0)}).$$

With field samples of decapods, t (age in years) and t_0 are not separately determinable, but estimates of L_∞ and k have been obtained from mark–recapture data, again by several methods (references in legend to Fig. 4). In our study we had available data for both carapace length increment G_M and molt interval I_{MM} for each molt cycle. This enabled us to estimate by least-squares regression for each L–E category the dependence of instantaneous carapace length growth rate G (on the assumption of eq. (1), text) upon carapace length l, and thereby obtain estimates of L_∞ and k.

From eq. (1) and (A3) we may derive an estimate of G for each molt cycle in terms of growth increment G_M at its conclusion and molt interval $\Delta t = I_{MM}/365$:

$$\text{(A4)}\quad \begin{aligned} G_M &= l_{T+\Delta t} - l_T \\ &= L_\infty\, e^{-kT}\,(1 - e^{-k\Delta t}) \\ &= (L_\infty - l_T)(1 - e^{-k\Delta t}) \end{aligned}$$

$$\text{(A5)} \quad G = \frac{dl}{dt} = \frac{kG_{\mathrm{M}}}{1 - e^{-k\Delta \mathrm{t}}}$$

where $\mathrm{T} = \mathrm{t} - \mathrm{t}_0$ and l_{T} is the carapace length during the molt cycle. $\hat{k}$ is initially estimated from the l coefficient in the G_{MM} regression (Table 6). An initial estimate of G by eq. (A5) is then made for each molt cycle and the G regression of Table 7 calculated:

$$\text{(A6)} \quad G = a - \hat{k}l + \mathrm{bT}_{\mathrm{MM}}.$$

Thus a new value for $\hat{k}$ is obtained. The G regression is then iteratively approximated by substituting the new value obtained for $\hat{k}$ and recomputing G (eq. (A5)) for each molt cycle and then recomputing the G regression upon l and T_{MM} (eq. (A6)). Typically, only three iterations were required to obtain agreement between old and new values of k to four significant figures. $E = kL_\infty$ (eq. (1)) is then obtained by summing $a + bT_{\mathrm{MM}}$ (eq. (A6)).

Appendix 3. SLOUGH and HATCH Categories

Figure 3 displays the distribution of embryo retention interval duration in dd_6 (D_{ER}) from experimental molt cycles containing an extrusion. The strong bimodality suggested dividing the distribution into two: "SLOUGH" ($D_{\mathrm{ER}} < 1000\ \mathrm{dd}_6$) and "HATCH" ($D_{\mathrm{ER}} > 1000\ \mathrm{dd}_6$) although a few of the HATCH category extrusions were known to have been completely shed prior to actual hatching.

Although the same percentage of hybrid extrusions (i.e. following matings with male *H. gammarus*, 41%) as homotypically derived ones (40%) belonged to the SLOUGH category, the mean D_{ER} for the hybrid clutches in this category was significantly longer ($\bar{x} = 513.6$ and $360.0\ \mathrm{dd}_6$, respectively; $F = 4.12$, df 1,41, $p < 0.05$). The mean D_{ER} for the hybrid clutches in the HATCH category was lower, although not significantly so ($\bar{x} = 1427.5$ and $1526.9\ \mathrm{dd}_6$, respectively; $F = 3.73$, df 1,62, $0.1 > p > 0.05$). Both effects appeared to result from a greater number of intermediate D_{ER} durations for the hybrid clutches ($700 \leqslant D_{\mathrm{ER}} < 1200\ \mathrm{dd}_6$, $n = 11$ and 3, respectively; the difference in number was not significant). Thus there was somewhat greater separation between the SLOUGH and HATCH distributions for the homotypically derived extrusions, but otherwise little difference.

None of the SLOUGH category eggs displayed eyespots, which normally appear 300–400 dd_6 after fertilization (Perkins 1972). Some SLOUGH category extrusions may have represented failures of fertilization. D_{ER} duration was always less than 500 dd_6 for confirmed "backcross" clutches (Fig. 3), i.e. those following matings to sterile hybrid *H. gammarus* × *H. americanus* males, which produce spermatophores lacking sperm (Talbot et al. 1983).

Ovarian resorption in lobsters is characterized by the sudden appearance of green-tinged hemolymph, visible externally as a green venter. This condition, which may be manifest for many weeks, reflects a very high concentration of lipoproteins in the hemolymph (Byard and Aiken 1984), including two lipoproteins not found in normal vitellogeneses which are similar to but immunologically distinct from the two characteristic of vitellogeneses (Nelson 1986; Nelson et al. 1988b). We observed such periods of green venter in 36% of L, NoE molt cycles studied but not at all in NoL, NoE molt cycles. They were observed to begin with equal probability at any molt cycle phase except within ±600 dd_6 of the molt, and lasted an average of 3.0 ± 2.0 consecutive 30-d observations. In 18% of the HATCH molt cycles as well, brief periods of green venter were seen. But they were confined to a period of 800–1400 dd_6 post-L, were never seen in consecutive observation periods, and appeared rather to represent brief preextrusion peaks in hemolymph vitellogenin titers accompanying normal vitellogeneses.

The SLOUGH category was intermediate in all respects. Green venter was observed in 25% of SLOUGH molt cycles, at all phases except within ±600 dd_6 of the molt, but more frequently between 800 and 1400 dd_6 post-L. An episode lasted an average of 1.75 ± 1.22 consecutive observations. The differences in timing and duration of green venter episodes between the SLOUGH and HATCH categories suggest that certain of the SLOUGHed clutches were products of abortive vitellogeneses, ovulations, or extrusions. Fifty-eight percent of the SLOUGHed extrusions discovered in green venter molt cycles were noted as very small or showing poor adhesion to the ovigerous setae at the time of their discovery; the corresponding figure for SLOUGH category molt cycles in which a green venter was not observed was 25%, and we noted only one case of poor initial adhesion for a HATCH category molt cycle.

A Hydrophobic Large-Volume Sampler for Collecting Aquatic Surface Microlayers: Characterization and Comparison with the Glass Plate Method

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Hardy, J. T., J. A. Coley, L. D. Antrim, and S. L. Kiesser. 1988. A hydrophobic large-volume sampler for collecting aquatic surface microlayers: characterization and comparison with the glass plate method. Can. J. Fish. Aquat. Sci. 45: 822–826.

The atmosphere–water interface represents a vital biological habitat and a collection point for natural and anthropogenic materials originating in the atmosphere and the water column. A Teflon-coated aluminum rotating drum sampler was constructed and tested. This sampler rapidly collects large-volume samples of the aquatic surface microlayer (uppermost 34 μm). The collection characteristics of the sampler are similar to those of the more time-consuming glass plate technique. Samples from estuarine, coastal, and offshore areas are generally highly enriched in selected organic compounds, metals, and microorganisms as compared with the subsurface bulk seawater. The sampler provides an efficient means of collecting hydrophobic pollutants from the water surface.

L'interface eau–atmosphère constitue un habitat biologique très important et un point de collecte pour des matériaux d'origine naturelle et anthropogénique produits dans l'atmosphère et dans la colonne d'eau. Un échantillonneur à tambour rotatif d'aluminium recouvert de Teflon a été construit et mis à l'essai. Il recueille rapidement des échantillons de fort volume de la microcouche superficielle (les 34 μm supérieurs). Ses caractéristiques de prélèvement sont identiques à celles de la technique de la plaque de verre, qui prend plus de temps. Les échantillons prélevés dans les zones estuariennes, côtières et hauturières sont généralement très riches en certains composés organiques, métaux et microorganismes par rapport à l'eau de mer qui se trouve sous la surface. L'échantillonneur constitue un moyen efficace pour prélever les polluants hydrophobes à la surface de l'eau.

Received February 24, 1987
Accepted January 12, 1988
(J9152)

Reçu le 24 février 1987
Accepté le 12 janvier 1988

The sea-surface millilayer (SMIL) (uppermost 1 mm or less of the water column) is the primary point of exchange for gases and materials cycling between the atmosphere and hydrosphere and covers more than 71% of the earth's surface. It provides a vital habitat for microorganisms (Carlucci et al. 1985) as well as for the eggs and larvae of many species of fish and shellfish (Zaitsev 1971). The sea surface also serves as a collection point for pollutants that, because of their hydrophobicity or association with floatable particles, concentrate in the sea-surface microlayer (SMIC), the uppermost 50 μm of the sea surface (Hardy 1982; Hardy and Word 1986; Hardy et al. 1986; Cross et al. 1987; Hardy et al. 1987). The presence of natural biogenic films in many areas alters the chemical properties of the sea surface (Williams et al. 1986) and serves to further concentrate hydrophobic contaminants, resulting in toxic effects on floating fish eggs (Hardy et al. 1986). Such films may also modify the optical properties of the sea surface in terms of remote sensing (Hartwig and Herr 1984). Despite its important characteristics, there are few adequate techniques for collecting large-volume samples of the SMIC for biological or chemical analysis.

More than 20 different techniques have been used for SMIC sampling (Hardy 1982). Each has its own unique characteristics and advantages or disadvantages (Carlson 1982; Garrett and Duce 1980; Huhnerfuss 1981). Hydrophilic rotating samplers include the ceramic drum, which samples the upper 60–100 μm of the water surface (Harvey 1966), and PVC drum, which samples the upper 250 μm (Brockmann et al. 1976) or 80 μm (Daumas et al. 1976), and the glass cylinder, which samples the upper 50–100 μm layer (Carlson et al. 1988).

Hydrophilic Teflon has been used to collect small-volume samples from aquatic surface microlayers. Hydrophilic Teflon (so-called bondable Teflon) is treated with sodium in liquid ammonia to produce a slightly etched surface. When immersed in water, this material becomes coated with a film distributed evenly over the entire surface. Although it is effective at collecting organic compounds such as oleic acid from the water surface, the organic film is considerably diluted with water during sampling (Garrett and Barger 1974). Hydrophilic samplers are poor collectors of lipid-type surface films.

Hydrophobic Teflon, on the other hand, preferentially collects hydrophobic organic compounds (a group that includes

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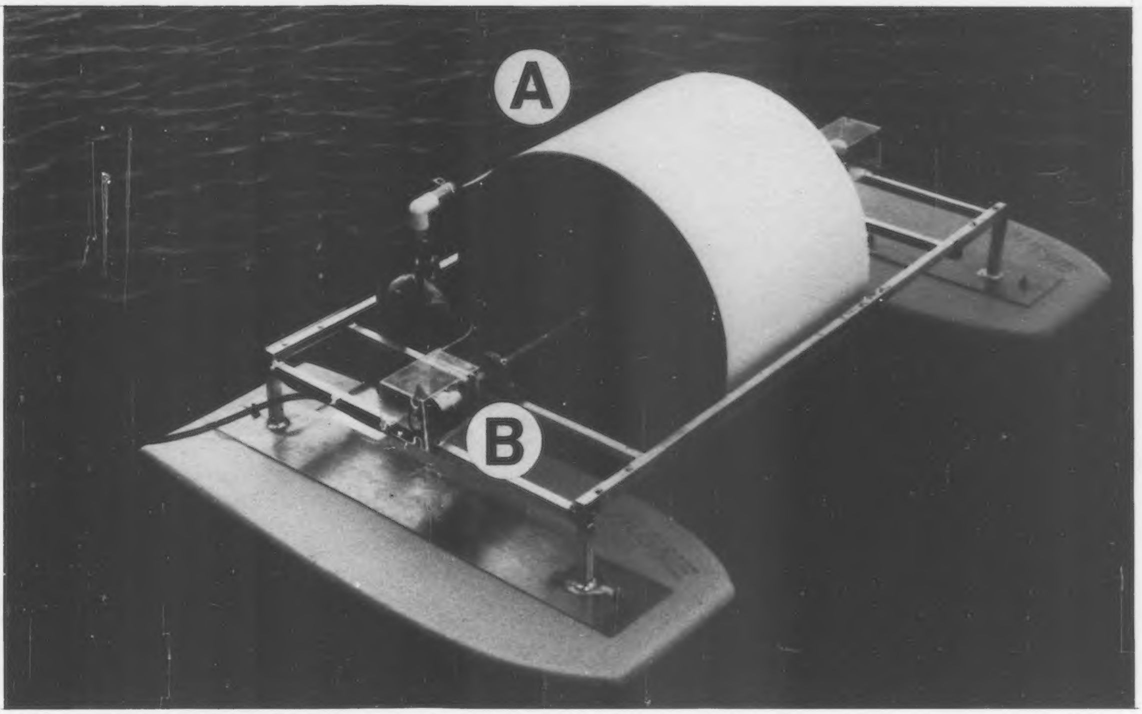

FIG. 1. Teflon-coated aluminum rotating drum for collecting samples of the sea-surface microlayer. A, squeegee; B, DC gearmotors.

many anthropogenic pollutants) and smaller quantities of water than the hydrophilic Teflon. In the absence of hydrophobic organics, hydrophobic Teflon will pick up small quantities of water distributed as a film of uneven thickness. Comparative studies have suggested that a thin film with associated microorganisms and hydrophobic compounds can be collected intact only by means of hydrophobic samplers (Kjelleberg et al. 1979). Hydrophobic membrane filters and Teflon sheets have been used to collect small-volume samples of the microlayer (Kjelleberg et al. 1979), but no efficient large-volume hydrophobic sampler has been evaluated. Our objective was to develop a hydrophobic sampler to conveniently and rapidly collect large-volume (3–4 L) samples of the upper 50 μm or less of the sea surface for subsequent microbiological and chemical analyses.

Methods

We constructed and tested a Teflon-coated rotating aluminum drum sampler. The collecting surface of the drum is coated with a hydrophobic Teflon film (a vinyl-supported self-adhesive overlay made by Norton Chemplast, Wayne, New Jersey). The drum is constructed of welded 1.29-mm aluminum and is 46 cm in diameter by 61 cm long. It is mounted in a frame of 1.9-cm-square aluminum tubing that is welded and bolted together and supported in the water by two foam "boogie board" floats (Fig. 1). A 2.54-cm solid aluminum axle runs through pillow block bearings and connects the drum to an electric DC gearmotor at each end (Dayton No. 4Z836). The motors are connected in parallel through an insulated cable to a 12-V deep-cycle marine battery on board a small boat. The motors operate at a gear ratio of 267.5 to 1 and turn the drum at 8.75 rpm. Thus, in operation the rotating drum sweeps a surface area of 10.21 $m^2 \cdot min^{-1}$ with a vertical withdrawl rate of about 21 $cm \cdot s^{-1}$. A 32-mm-thick neoprene rubber squeegee riveted between an aluminum angle and a PVC angle (top plate) and slanted across the back of the drum removes the microlayer from the drum. The squeegee is spring mounted to provide uniform tension against any irregularities in the rotating drum. The sample drains along the PVC angle at the back of the squeegee, through a PVC elbow at the end, and into a 4-L glass collecting jug.

The sampler is designed to hold one sample container during each operation. The 4-L sample bottles are cleaned appropriately for the type of sample to be collected. When samples are to be used for chemical analysis, bottles are rinsed with 200 mL of methylene chloride, air dried, acid cleaned for 24 h in 5% ultragrade nitric acid, rinsed well with glass-distilled water, and then dried in a laminar flow hood. To minimize contamination of the drum sampler, it is covered by a protective polyethylene tarp during transport aboard vehicles or boats to exclude, as well as possible, atmospheric dust and soot. The small boat used to deploy the sampler is cleaned inside and out with detergent and rinsed well prior to sampling. Gasoline cans and any other sources of obvious contamination are removed from the vicinity of the operation. During sampling an electric trolling motor drives the boat forward through the sampling site.

The sampler is deployed from a small boat by placing it on an extension beam at a distance of 1–2 m from the forward and windward beam of the boat. Before each set of replicate samples (i.e. at each sampling site), the Teflon surface of the drum is cleaned with a detergent solution and soft sponge and then

TABLE 1. Comparison of partition-infrared measurable oils (American Public Health Association 1976) in glass plate and drum samples collected from Puget Sound.

Location	Sample type	Oil concentration ($mg \cdot L^{-1}$) Drum	Plate	Bulkwater	Mean ratio (microlayer/bulkwater)[a]
Sequim	Slick	1.4	0.26		6.3
Bay		0.34	0.34		2.6
(rural)				0.13	
	Nonslick	1.05	0.14		4.6
		0.49	0.59		4.2
Elliot	Slick	45	17		221
Bay		12	16		100
(urban)				0.14	
	Nonslick	1.9	1.4		11.8
		2.1	1.1		11.4

[a] Concentration in microlayer divided by concentration in bulkwater.

rinsed with bulk seawater from the site. The drum is rotated for 2–3 min to rinse it and the squeegee well with ambient microlayer before the glass sample jug is attached. The boat is driven slowly forward by the electric motor at a speed to match the rotation of the drum ($\sim 1\ km \cdot h^{-1}$). The duration of sample collection is recorded with a stopwatch. When 3–4 L of microlayer has been collected, the sampler is turned off and the sample retrieved. Sampling transects may be circular, follow a predetermined grid, or be biased toward sampling inside or outside areas of high surface pressure (visible slicks). Because patchiness in surface microlayer chemistry is frequently encountered, at least two replicate samples are collected from each sampling station. In environmental studies, reference samples are collected from areas believed to be low in contamination. When operating from a larger "mother" vessel, the reference samples are collected from a small boat positioned at least 100 m away from the windward side of the larger vessel to avoid contamination.

Ancillary sea-surface data include near-surface wind speed (with a hand-held anemometer), Beaufort sea state (Maloney 1977, p. 255–257), water temperature, and surface film pressure. The latter is measured by the oil drop spreading method (Adam 1937).

Laboratory experiments were conducted to determine the collection efficiency of the Teflon drum. Radiolabelled [^{14}C]DDT dissolved in oleyl alcohol was used to represent a dry surfactant that forms monolayers. The microlayer samplers consisted of three mini-drum samplers constructed to about one sixth of the scale used in actual field sampling devices. The mini-drums had surface areas of 132–137 cm^2.

Experiments were conducted at three surface pressures. Three solutions were prepared with concentrations of oleyl alcohol dissolved in hexane of 0.5, 1.0, and 1.5 $mg \cdot L^{-1}$. [^{14}C]DDT (100 μL) was added separately to 12 mL of each of the above solutions. A 1-mL sample of this solution (3.456×10^6 dpm) was added to the surface of each of three pyrex glass trays (surface area 704 cm^2) containing 2960–3020 mL of deionized water and allowed to spread. Thus, trays 1, 2, and 3 had increasing quantities of oleyl alcohol on the water surface. Following evaporation of the hexane (10 min) the surface film was sampled by one rotation of the mini-drum, i.e. 19.43% of the surface area of the tray. Following collection, the drum surface was rinsed with a measured volume (23–41 mL) of methylene chloride and the rinse collected in a beaker. Rinse (0.5 mL) was added to each of three replicate scintillation vials and counted in a scintillation counter. Counts were corrected for background and for quenching using the external standards ratio technique.

Results and Discussion

In the laboratory experiments on collection efficiency, counts of ^{14}C indicated a recovery of 79–88% for DDT. Recovery increased with increasing film pressure and was 79, 80 and 88% for mean surface pressures of 4.6, 19.6, and >23 $mN \cdot m^{-1}$, respectively. This represents the minimum collection efficiency of the drum, since any loss to the subsurface water or walls of the tray would decrease the expected quantity of DDT recovered by the drum.

We compared the sampling characteristics of the Teflon drum with the glass plate technique described previously (Harvey and Burzell 1972; Hardy et al. 1985). In Puget Sound, samples were collected with both plate and drum at slick and nonslick stations in urban and rural bays. The measured concentrations of oil and grease were, on average, 45 times greater in the microlayer than in the bulkwater (Table 1).

The thickness of the surface microlayer sampled was estimated by dividing the surface area swept by the drum by the volume of sample collected. For 24 samples collected over a wide range of surface pressures (6–21 $mN \cdot m^{-1}$), the sample depth ranged from 6 to 66 μm with a mean of 34 μm (SD ± 18.3). Microlayer samples were collected at stations 150 mi (241 km) offshore from Daytona Beach, Florida (Blake Plateau), using both the Teflon drum and the glass plate method. Results from both methods indicated that concentrations of metals analyzed by atomic absorption spectrophotometry (Hardy et al. 1985) were, on average, 3–12 times greater in the microlayer than in the bulkwater (Table 2).

The rotating drum sampler provides a large-volume sample in a short period of time, a major advantage compared with the slow and tedious glass plate method. Depending upon the quantity of surface active organics, the drum collects approximately 100–400 $mL \cdot min^{-1}$ whereas the glass plate collects only about 10–40 $mL \cdot min^{-1}$.

We examined the significance of differences between the collection characteristics of the drum and the glass plate using the Wilcoxon matched-pairs signed-rank test (Zar 1974). This test was chosen because we have paired data (drum and plate) that appear to be nonparametric in distribution between sampling sites; that is, the concentrations of oil or metals are very high in a few samples, but relatively low in most samples. We were unable to detect a significant ($p < 0.05$) difference in the concentrations of infrared measured oils in eight pairs of samples (Table 1) or in the concentrations of dissolved or particulate metals in nine pairs of samples (Table 2, samples 2 and 4) collected by the two methods.

Phytoneuston, microalgae inhabiting the aquatic surface microlayer, form an important and often abundant community. They have been collected effectively using the glass plate technique (Hardy and Apts 1984), and their densities are typically 10 to several hundred times greater than that of the phytoplankton in the bulkwater (Hardy 1982). The Teflon drum was also a good collector of phytoneuston from a visible natural slick at the offshore Atlantic site (Table 3). A very different community was found to inhabit the microlayer compared to the bulkwater. The enrichment ratio (concentrations of phytoneuston/phytoplankton) was 390.

TABLE 2. Concentration ($\mu g \cdot L^{-1}$) of metals in microlayer and bulkwater at an offshore (Blake Plateau) station (detection limits $<0.3\ \mu g \cdot g$ dry wt^{-1} for particulate and $<0.05\ \mu g \cdot L^{-1}$ for dissolved metals).

Sample number	Type[a]		Ni	Cu	Cd	Pb	Zn
Drum							
1	No slick	D	2.14	2.52	1.18	1.39	31.19
		P		0.10	0.01	0.03	0.60
		T		2.62	1.19	1.42	31.79
2	In slick	D	3.06	3.40	1.01	0.72	30.33
		P		0.52	0.45	0.23	1.85
		T		3.92	1.46	0.95	32.18
3	Integrated slick and nonslick transect	D	0.50	1.24	0.22	0.37	5.60
		P		0.11	0.00	0.03	0.29
		T		1.35	0.22	0.40	5.89
Plate							
4	In slick	D	2.07	4.32	0.96	1.21	34.61
		P		1.16	0.01	0.62	2.24
		T		5.48	0.97	1.83	36.85
5	Bulkwater under slick	D	0.35	0.67	0.12	0.26	4.82
		P		0.00	0.00	0.03	0.28
		T		0.67	0.12	0.29	5.10
	Microlayer enrichments[b]		5.82	11.86	3.28	6.31	

[a] Dissolved (passing through a 0.4-μm filter); P, particulate; T, total.

[b] Total in sample 2 divided by total in sample 5.

TABLE 3. Concentrations (individuals$\cdot L^{-1}$) of microorganisms collected with the drum from a visible slick at the Blake Plateau (total count of more than 250 individuals made on each sample; minimum detection (based on one individual) is $252 \cdot L^{-1}$ for the microlayer and $20 \cdot L^{-1}$ for the bulkwater).

		Sample	
	Taxon	Microlayer	Bulkwater
Diatoms	*Achnanthes* sp.	3 632	
	Chaetoceros spp.		220
	Nitzschia closterium	10 169	
	Nitzschia pungens		140
	Thalassiosira sp.	242	
	Unidentified pennates	11 136	1380
Dinoflagellates	Unidentified heterotrophs	1 211	
	Unidentified autotrophs	7 262	460
	Amphidinium spp.		120
	Dinophysis spp.		40
	Exuviella sp.	242	
	Gymnodinium fuscum		60
	Prorocentrum sp.		20
Euglenoids	*Euglena* sp.	3 632	
Microflagellates	Unidentified autotrophs	2 138 542	3180
	Unidentified heterotrophs	6 053	
Blue-green algae	*Trichodesium* sp.	18 644	
Microzooneuston	Other ciliates	2 420	
	Rotifers	242	
	Tintinnids	6 053	
	Total autotrophs	2 193 501	5620

Rotating drum samplers, which provide an efficient method for collecting large-volume samples of the SMIC, collect a surface layer one fourth to one tenth as thick as the screen method (300–400 μm). Enrichments (i.e. SMIC/bulkwater concentrations) for microorganisms, pigments, ATP, particulate organic matter, and alkanes are greater on the basis of drum sampling than on screen sampling (Daumas et al. 1976). Particles accumulate at the air–water interface, whereas dissolved substances may be distributed throughout a thicker layer (Daumas et al. 1976). Since hydrophobic organic and metal pollutants in aquatic ecosystems are largely associated with particles, the hydrophobic sampler provides the preferred method for assessing water surface contamination.

We have used the drum to collect over 200 samples in rivers, estuaries, bays, and offshore areas. These samples have been examined for concentrations of hydrophobic oils and grease, metal and organic pollutants, microorganisms, and materials toxic to fish eggs and have also been compared with bulkwater samples collected from a depth of 20 cm. Details of many of these analyses and results are described elsewhere (Hardy et al. 1986; Cross et al. 1988; Hardy et al. 1988). In general, microlayer samples tended to have much higher concentrations of contaminants, especially in visible slicks near urbanized coastal areas. The Teflon-coated rotating drum microlayer sampler collects a relatively thin layer (~34 μm) and is comparable in collection characteristics to the more time-consuming glass plate technique.

We have examined possible sample contamination originating from the sampler itself. Samples of distilled water collected with the drum showed no detectable levels of the contaminants measured (i.e. metals, PCBs, aromatic or saturated hydrocarbons). However, the risk of contamination from the sampler could be reduced even further in future versions by incorporating a Teflon squeegee and coating the entire aluminum frame with Teflon.

The Teflon drum preferentially collects hydrophobic lipid-type films and may discriminate against polar surface-active material. It is particularly useful in studies of water surface contamination where large-volume samples of surface film and associated hydrophobic pollutants are required for chemical analysis.

Acknowledgments

This work was supported by the National Oceanic and Atmospheric Administration under a Related Services Agreement with the U.S. Department of Energy Contract DE-AC06-RL0 1830 and in part by the U.S. Environmental Protection Agency. Edward Long (National Oceanic and Atmospheric Administration), David Redford (Environmental Protection Agency), and Jack Word (Battelle, Pacific Northwest Laboratories) provided helpful encouragement and suggestions during the development of these methodologies. We thank Rita Horner (University of Washington) for assistance in identifying microneuston species.

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Comparative Physiological Ecology of Centrarchids in Hyposaline Environments[1]

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Empirical evidence and data from this study suggests that there are intrafamilial differences in salinity tolerance that apparently change longitudinally along salinity gradients. *Lepomis punctatus* and *Micropterus punctulatus* require a significantly longer time to acclimate to increased salinity than *L. microlophus*, which apparently acclimates within 1 h. Both increased salinity (0–8 ppt) and the time (1–72 h) exposed to a particular salinity impact osmotic and hematocrit regulation. Observed intrafamilial differences in osmotic and hematocrit regulation underlay the distribution and relative abundance of centrarchids and could explain their seasonal use of low-salinity marshes. Furthermore, the >12-h acclimation times of *L. punctatus* and *M. punctulatus* suggest that these two species may never become fully acclimated to a salinity during a diurnal tidal cycle.

Les indications empiriques et les données fournies par cette étude semblent montrer qu'il existe, au sein d'une même famille, des différences dans la tolérance à la salinité qui apparemment changent longitudinalement le long des gradients de salinité. Il faut à *Lepomis punctatus* et à *Micropterus punctulatus* nettement plus de temps pour s'habituer à une augmentation de la salinité que ce n'est le cas pour *L. micropholus*, qui semble s'acclimater en 1 h. L'augmentation de la salinité (0 à 8 ppt) et la durée (1 à 72 h) d'exposition à une salinité donnée ont toutes deux un effet sur la régulation osmotique et de l'hématocrite. Les différences observées au sein d'une famille dans la régulation osmotique et de l'hématocrite sous-tendent la répartition et l'abondance relative des centrarchidés et pourraient expliquer leur présence saisonnière dans des marais à faible salinité. En outre, la durée d'acclimatation de *L. punctatus* et *M. punctulatus* (>12 h) indiquerait que ces deux espèces ne peuvent s'adapter totalement à la salinité pendant un cycle de marée diurne.

Received September 28, 1987
Accepted February 5, 1988
(J9438)

Reçu le 28 septembre 1987
Accepté le 5 février 1988

Low-salinity marshes are major components of many Atlantic and Gulf Coast estuarine systems, although they are considered low-diversity habitats in terms of secondary production (Khlebovich 1969; Remane and Schlieper 1971). However, members of the freshwater fish family Centrarchidae can numerically dominate these marsh systems (Keup and Bayless 1964; Hackney and de la Cruz 1981; Rozas and Hackney 1984). Centrarchids have also been shown to reproduce in salinities ranging up to 4.5 ppt (Tebo and McCoy 1964).

Freshwater fishes that invade habitats of increasing salinity reduce the osmotic gradient between their plasma and the environment. Associated with this reduction is an increase in osmolality, a decrease in hematocrit, increased drinking, and decreased oxygen consumption rates (Lutz 1972; Norton and Davis 1977; Leray et al. 1981). In some teleosts, a reduced gradient has been shown to be energetically less costly, with metabolic rate reductions ranging between 20 and 45% (Rao 1968; Farmer and Beamish 1969; Maceina et al. 1980; Furspan et al. 1984). A major contribution to reduced energy expenditure as freshwater fishes move into higher salinity has been attributed to the reduction of energy used to produce a dilute urine (Furspan et al. 1984).

If abiotic conditions are important structuring factors for centrarchids, then intrafamilial differences in the use of and abundance in various habitats along the gradient can be quantified and are potentially based upon variation in physicochemical factors. Furthermore, the distribution of many metazoans along salinity gradients can be regulated either by their osmoregulation capabilities (Roddie et al. 1984; McNamara 1987) or habitat selection (Barnes 1967). Presently, there is no information concerning the osmoregulatory responses of centrarchids to various salinities. Thus, this study determines and compares the (1) time course of osmotic and hematocrit acclimation to various salinities and (2) osmoregulatory and hematocrit patterns in these salinities for the redear sunfish (*Lepomis microlophus*), spotted sunfish (*L. punctatus*), and spotted bass (*Micropterus punctulatus*). I also examined salinity tolerances of selected centrarchids and compared these with the experimental data.

Materials and Methods

Field Collections and Laboratory Protocol

Centrarchids were collected by bag seine between May and September 1985 and 1986 from Old Fort Bayou, a tidal river of the Biloxi Bay estuary, Mississippi (USA). Collections were made at numerous locations in both tidal freshwater and oligohaline sections of the river. Fish were transported to the laboratory in aerated, insulated styrofoam coolers containing Old Fort Bayou water. They were held in the coolers in the laboratory at 25.0 ± 1.0°C overnight. Individuals were then transferred to 38-L covered aquaria containing dechlorinated (aerated) tap water. Each aquarium was equipped with a heater, aerator, and filter. The fish were held in freshwater and exposed to a 14 h light : 10 h dark photoperiod for 7 d prior to experimentation. Fish were fed a meal of live earthworms and/or shrimp pellets once every other day. Five experimental aquaria were established ranging from 0 to 8 ppt in 2-ppt salinity increments. Experimental salinities were produced using dechlorinated tap water and Instant Ocean Sea Salts. Salinities were checked daily using an AO refractometer or a YSI model 33 S-C-T meter.

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Osmoregulation/Hematocrit Experimental Procedures

Two experiments were conducted to show the (1) time course of osmotic and hematocrit acclimation and (2) osmoregulation and hematocrit responses across salinity treatments. Individuals fasted for 24 h were transferred to experimental aquaria at salinities of 0, 2, 4, 6, and 8 ppt. At time intervals of 1, 4, 8, 12, 24, 36, 48, 60, and 72 h after abrupt transfers, plasma osmolality and hematocrit determinations were made. The following controls were used for each experiment: (1) individuals held in freshwater for 7 d were used at each time course experiment and (2) one of the time course experiments (0 ppt) examined the response of the individuals to the transfer process (freshwater to freshwater). Up to five individuals for each salinity and time combination (see figure legends for specific details) were examined as follows. Blood samples were obtained by first blotting each individual dry and then severing its caudal fin with a razor (Barton 1979; Wakeman and Wohlschlag 1983). The incision was immediately blotted and blood from the caudal artery was drawn into a heparinized microcapillary tube and centrifuged for 4 min at 11 500 rpm in an International microcapillary centrifuge (model MB) for hematocrit determination. Plasma collection was completed within 1 min to avoid handling effects on osmolality (Robertson et al. 1987). Subsequently, plasma in the microcapillary tube was separated from the formed elements by breaking the tube at the boundary. Plasma osmolality (milliosmoles per kilogram) was then determined on a Wescor vapor pressure osmometer (model 5100). A total of 620 hematocrit and osmolality determinations were made (see details in figure legends). Based upon these time course studies, 48-h values were used to examine changes in osmoregulation and hematocrit across the salinity treatments.

Statistical Analyses

Fish size and the osmolality and hematocrit responses (time course, across salinities and between species) were compared by ANOVA ($\alpha = 0.05$) and a Newman–Keuls (N-K) multiple range test ($\alpha = 0.05$) (Klockars and Sax 1986). These analyses were performed using the SPSS^x 2.1 program package (SPSS Inc. 1985). Variation within and among responses was described by the coefficient of variation (CV).

Results

Individuals ranged between 3.6 and 10.5 cm standard length (SL) depending upon species, salinity, and time periods. There

TABLE 1. Coefficient of variation for the 48-h osmolality and hematocrit values across salinity treatments. C = fishes held in freshwater for 7 d (control).

Species	Treatment (ppt)	Osmolality ($mosmol \cdot kg^{-1}$)	Hematocrit
L. microlophus	C	20.29	3.14
	0	22.34	6.82
	2	22.13	6.32
	4	5.34	4.66
	6	17.96	3.16
	8	22.33	6.86
L. punctatus	C	7.63	4.27
	0	9.90	3.94
	2	13.70	3.42
	4	21.01	12.38
	6	8.09	0.93
	8	9.88	2.58
M. punctulatus	C	9.56	1.85
	0	9.12	1.63
	2	15.12	2.74
	4	4.86	4.51
	6	6.37	4.00
	8	15.41	5.01

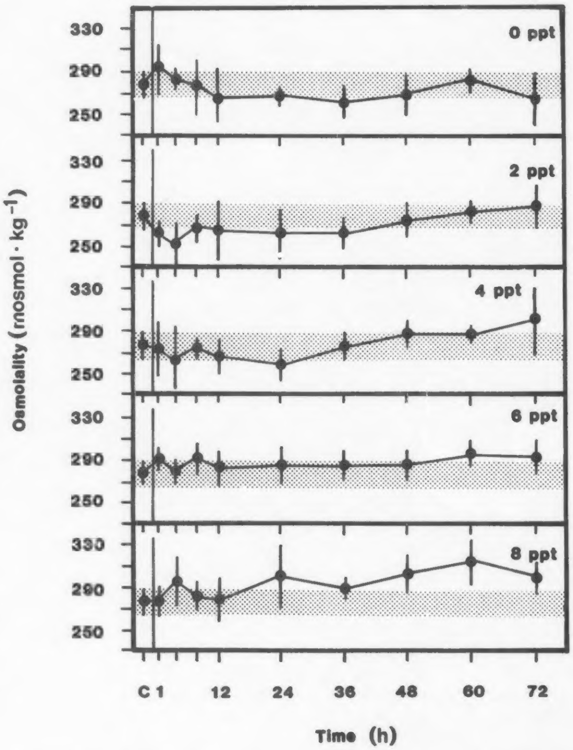

FIG. 1. Osmolality ($\bar{X}$ + SD) time course curves for *L. microlophus* in salinities from 0 to 8 ppt and time periods from 1 to 72 h. C = control fishes held in freshwater for 7 d. The horizontal shaded area is the control ($\bar{X}$ + SD) response and is used for comparative purposes. Each mean value is based upon five individuals.

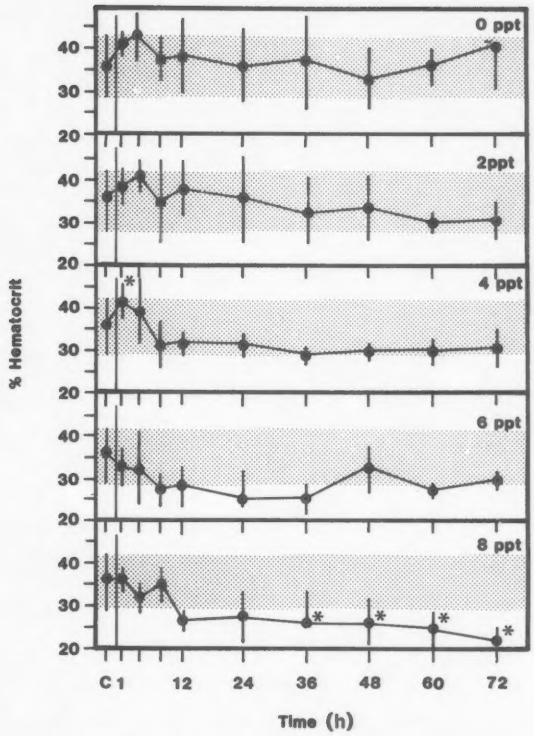

FIG. 2. Hematocrit ($\bar{X}$ + SD) time course response curves for *L. microlophus*. See Fig. 1 for details. Asterisks indicate significant differences from control (ANOVA; $p < 0.05$).

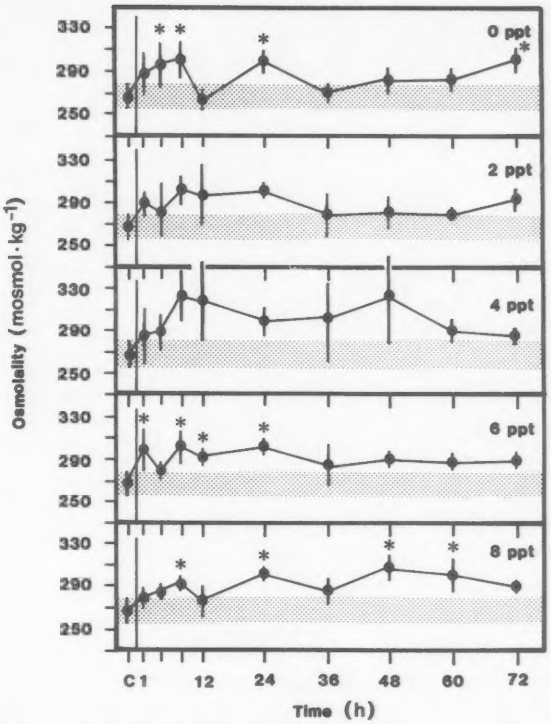

FIG. 3. Osmolality ($\bar{X}$ + SD) time course response curves for *L. punctatus*. Each mean value is based upon five individuals except for the 1- and 24-h periods for all salinities ($N = 4$) and the 72-h values in the 4- to 8-ppt treatments ($N = 4$). See Fig. 1 for details. Asterisks indicate significant differences from control (ANOVA; $p < 0.05$).

were no significant differences in the size of *L. microlophus* groups used for the time course or 48-h osmoregulation/hematocrit comparisons (ANOVA; $p > 0.05$). There were, however, size differences for *L. punctatus* and *M. punctulatus*. For the time course experiments, only the control group of *L. punctatus* was significantly larger than all others ($p < 0.05$). There were no differences ($p > 0.05$) among the 48-h across-salinity groups for *L. punctatus*. The 48-h across-salinity groups of *M. punctulatus* were not significantly different. However, within the 4-ppt time course experiment, the 8-h group was significantly smaller than the 48-h and control groups ($p < 0.05$). Additional comparisons were made of the 48-h within-salinity experiments. These indicate that there were no significant differences in size between the three species for the 0- or 6-ppt treatments ($p < 0.05$). However, the *L. microlophus* group was significantly larger than the other two species groups ($p < 0.05$) in the 2-ppt treatment, while *L. punctatus* was significantly larger than the other two species in the 4-ppt treatment ($p < 0.05$). *Micropterus punctulatus* was significantly larger than the other two species in the 8-ppt treatment ($p < 0.05$).

Different values among salinity treatments for *L. punctatus* and *M. punctulatus* suggest that these two species are more variable in their osmoregulatory ability than *L. microlophus*. At 48 h, osmolality and hematocrit values showed less variation among treatments for *L. microlophus* than for *L. punctatus* and *M. punctulatus* (Table 1). However, more within- and less among-treatment variation in osmolality noted for *L. microlophus* (Table 1) indicates that although they have a wider range in osmolality at a single salinity, they are more consistent across salinity treatments.

Generally, osmolalities of treated *L. microlophus* did not differ significantly from control values (Fig. 1). However, the 72-h value at 4 ppt was higher than the 24-h value (N-K; $p = 0.048$). Furthermore, at 48 h there were no differences across salinity values for *L. microlophus* ($p > 0.05$; see Fig. 7a). Similarily, no differences were found in hematocrit at 48 h across salinity treatments ($p > 0.05$; Fig. 7b). However, while hematocrit time course experiments for *L. microlophus* (Fig. 2) indicate no differences for the 0- and 2-ppt treatments ($p > 0.05$), significant differences ($p \leqslant 0.05$) were apparent in the 4- to 8-ppt treatments. Within the 4-ppt treatment, the 1-h hematocrit value was larger than all other values (N-K; $p < 0.05$). Although there was a significant F value in the 6-ppt treatment, no two groups were significantly different (N-K; $p > 0.05$). In the 8-ppt treatment, lower hematocrit values were found in the 36- to 72-h periods, when compared with the other time periods and with the control (Fig. 2).

Both osmolality and hematocrit values for *L. punctatus* and *M. punctulatus* were different than for *L. microlophus*. The two former species had considerably more significant deviations from control values. Except for the 2-ppt treatment, there were significant differences in all the osmolality values for *L. punctatus* at all measurement times (Fig. 3). The control was lower than the 4-, 8-, 24-, and 72-h time periods ($p < 0.05$) in the 0-ppt treatment (N-K; $p > 0.05$). Although there was a significant

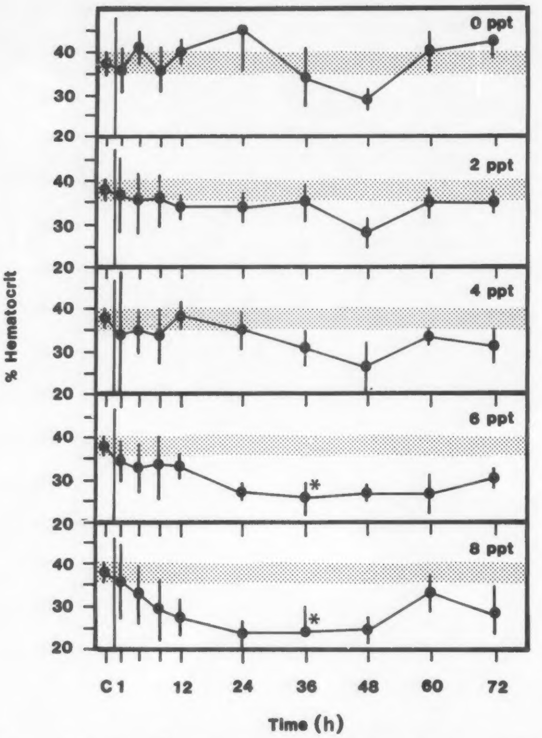

FIG. 4. Hematocrit ($\bar{X}$ + SD) time course response curves for *L. punctatus*. Each mean value is based upon five individuals except for the 1- and 24-h values in all salinities ($N = 4$) and the 72-h values in the 4- to 8-ppt treatments ($N = 4$). See Fig. 1 for details. Asterisks indicate significant differences from control (ANOVA; $p < 0.05$).

F value in the 4-ppt treatment, N-K indicates that no two groups were significantly different. In the 6-ppt treatment, the control was lower than the 1-, 8-, 12-, and 24-h values ($p < 0.05$), while in the 8-ppt treatment, the control was lower than values at 8, 24, 48, and 60 h ($p < 0.05$). Measured hematocrits (Fig. 4) indicate that there were no differences in the 2- and 4-ppt treatments ($p > 0.05$) for *L. punctatus*. A significant *F* value was found in the 0-ppt treatment, but N-K indicated that no two groups were different. In both the 6- and 8-ppt treatments, the controls were higher than the 36-h values (Fig. 4). The 48-h osmolality and hematocrit values were significantly different from each other ($p < 0.05$; Fig. 7a and 7b). The osmolality values at 4 ppt were higher than at the other salinities and the hematocrits of the controls were higher than those for all other salinity treatments ($p < 0.05$; Fig. 7b).

All salinity treatments for *M. punctulatus* osmolality time course experiments were significantly different ($p < 0.05$; Fig. 5). For the 0- to 4-ppt treatments, the controls were lower than the values at 8 h (N-K; $p < 0.05$). The 6- and 8-ppt treatment controls were lower than the values at 4, 8, and 48 h ($p < 0.05$). Comparison of the 48-h values (Fig. 7a) indicate that 4-, 6-, and 8-ppt treatments were significantly higher than the control and 2-ppt treatments ($p < 0.05$). There were no significant hematocrit time course differences ($p < 0.05$; Fig. 6) in the 0-ppt treatment for *M. punctulatus*; however, the 2-ppt treatment values were different but N-K could not distinguish them. For the 4-ppt treatment, the 24-, 36-, 60-, and 72-h values were significantly lower than the control values. The 4-, 8-, 12-, 24-, 36-, 60-, and 72-h values were lower ($p < 0.05$) than controls for both 6- and 8-ppt treatments (Fig. 6) and the 48-h value was lower in the 8-ppt treatment as well. The 48-h hematocrit time course values (Fig. 7b) indicate that the value at 8 ppt is significantly lower than the other salinity treatment values ($p < 0.05$).

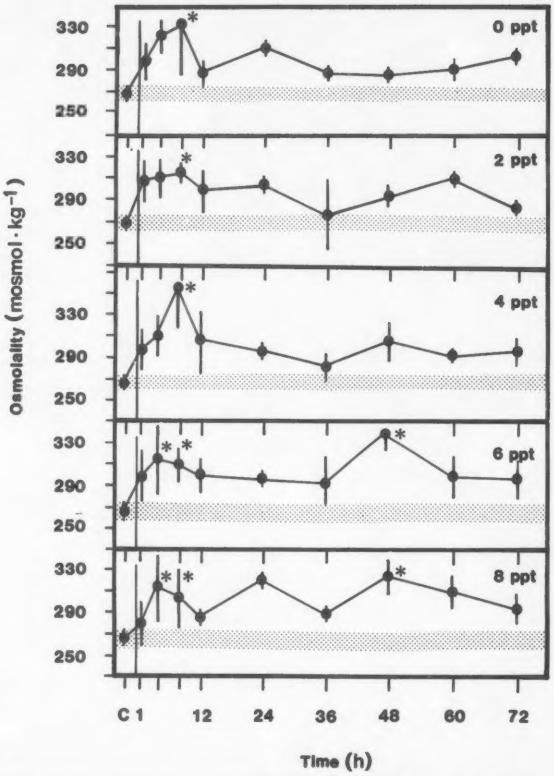

FIG. 5. Osmolality ($\bar{X}$ + SD) time course response curves for *M. punctulatus*. Each mean value is based upon five individuals for the 1-, 4-, 8-, and 48-h periods. $N = 4$ for the 12-h period in the 2- and 8-ppt treatments; $N = 3$ for the 4- and 6-ppt treatments. Both the 24- and 36-h periods were based upon two individuals in all salinities. The 60- and 72-h periods are based upon three individuals each in all salinities except the 8-ppt treatment in 60 h ($N = 2$). See Fig. 1 for details. Asterisks indicate significant differences from control (ANOVA; $p < 0.05$).

The general lack of significant differences in osmolality and hematocrit between species within salinity treatments appears to be due to the variation within and among treatments. There were no significant differences between species values in the 0-, 2-, 4-, and 8-ppt treatments ($p > 0.05$; Fig. 7a); however, in the 6-ppt treatment, *M. punctulatus* had a higher mean osmolality value than the other two species ($p < 0.05$). The 48-h within-salinity hematocrit values, however, are all significantly different except the 8-ppt treatment (Fig. 7b). In 0-, 4-, and 6-ppt treatments, *M. punctulatus* had significantly elevated hematocrits compared with the other two species ($p < 0.05$), while in the 2-ppt treatment, *M. punctulatus* was greater than *L. punctatus* (Fig. 7b).

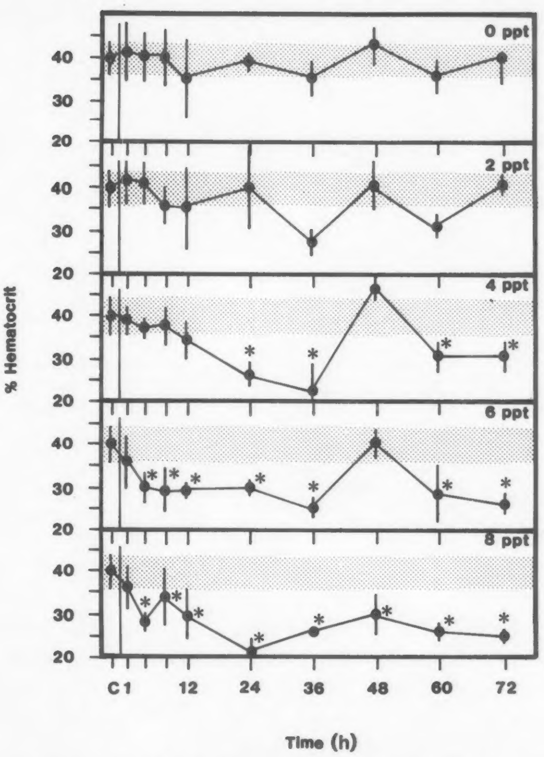

FIG. 6. Hematocrit ($\bar{X}$ + SD) time course response curves for *M. punctulatus*. See Fig. 5 for details. Asterisks indicate significant differences from control (ANOVA; $p < 0.05$).

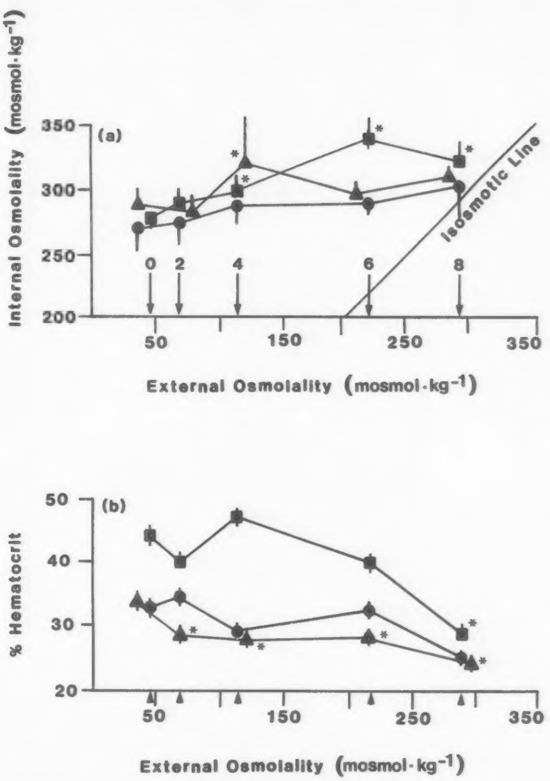

FIG. 7. (a) 48-h osmolality and (b) hematocrit responses across the salinity treatments. Values are expressed as the $\bar{X}$ + SD. ● = *L. microlophus*; ▲ = *L. punctatus*; ■ = *M. punctulatus*. The arrowheads represent the salinity treatments and the corresponding osmolality values. Some of the values were shifted laterally in order to make interpretation easier. All mean values are based upon five individuals. Asterisks indicate significant differences from control (ANOVA; $p <$ 0.05).

Discussion

Centrarchids are known to enter saline environments with two groups being apparent (Fig. 8): (1) those species that can tolerate high salinity and (2) those that cannot tolerate high salinity. The penetration of these fishes into saline habitats could depend upon the rate of salinity change rather than actual salinity. Peterson et al. (1987) showed that *L. macrochirus* exhibited klinokinesis when confronted with rapid salinity changes but exhibited orthokinesis when changes were gradual. The rate of salinity change within an estuary depends upon size, morphology, and latitude. Tidally regulated estuaries (daily estuaries) present more physiological challenges than do river-regulated systems (seasonal estuaries) because the latter have a slower rate of salinity change (Levinton 1982). Thus, centrarchids in seasonal estuaries could move into higher salinities than the same species in a daily estuary. Finally, the differential penetration among centrarchids could be due in part to the acclimatization process.

The time course experiments (osmolality and hematocrit) suggest that *L. punctatus* and *M. punctulatus* undergo an initial acclimation period characterized by significant increases in osmolality and decreases in hematocrit, while osmolality in *L. microlophus* does not significantly increase but hematocrit decreases in higher salinity treatments. Leray et al. (1981) indicated that rainbow trout (*Salmo gairdneri*) abruptly transferred to increased salinities underwent a ''crisis'' period that included increasing osmolality and a concomitant decrease in hematocrit. A ''stabilization'' period followed when cellular dehydration and electrolyte loads were eliminated through regulatory processes. A similar ''stabilization'' period was not noticed for either *M. punctulatus* or *L. punctatus* within the time frame examined.

There was also a clear difference in the salinity acclimation time for each species across the treatments examined. *Lepomis punctatus* acclimated to increased salinity within 36 h in all treatments except 8 ppt, where acclimation occurred within 72 h. In treatments of 0–4 ppt, *M. punctulatus* acclimated by 12 h, while in higher salinities, acclimation took at least 72 h. *Lepomis microlophus* apparently acclimated to all salinity treatments within 1 h. Although acclimation time course periods differ between these similar species, other confamilial species also show considerable variation (Natochin and Lavrova 1974). Evidence from other freshwater fishes suggests that a wide range of acclimation times, ranging from 8 h (Renfro and Hill 1971) to 6 d (Leray et al. 1981), is not unusual. Furthermore, acclimation times within euryhaline cyprinodontids range from several hours (Schmidt-Nielsen 1977) to several days (Stanley and Fleming 1977; Jacob and Taylor 1983). The difference in acclimation time suggests that *L. microlophus* should be able

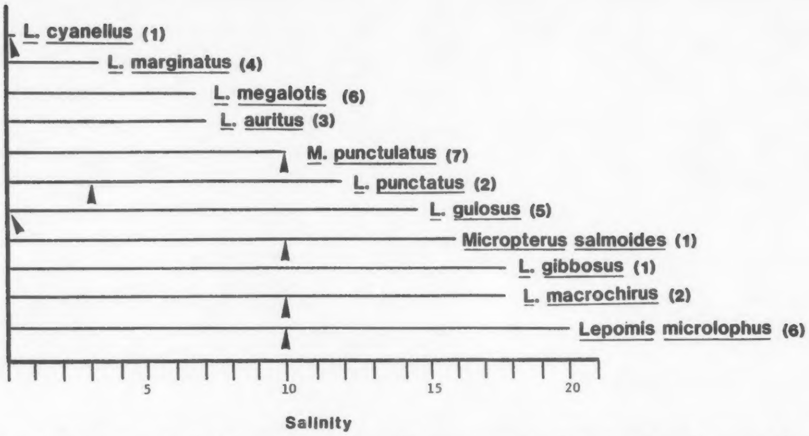

FIG. 8. Penetration of selected centrarchids into saline environments. Only those data that reported at least five individuals or a category of "occasional" for any salinity were included in this figure. "Rare" categories were not included. Symbols represent authority of data. 1 = Epperly 1984; 2 = Odum et al. 1984; 3 = Schwartz 1981; 4 = Keup and Bayless 1964; 5 = Swingle and Bland 1974; 6 = Christmas and Waller 1973; 7 = M. S. Peterson, unpubl. data. Arrowheads indicate highest salinity recorded by author.

to acclimate to higher salinity than either *L. punctatus* or *M. punctulatus*. This is further substantiated by examination of the upper salinity tolerances among centrarchids (Fig. 8).

The increasing plasma osmolality resulted in decreasing hematocrit with both increasing salinity treatment and time exposed to each salinity. The 48-h hematocrits also tended to "mirror" the osmolality values, particularly for *L. punctatus* and *M. punctulatus*. Reduced hematocrit values suggest cell shrinkage and dehydration (Lutz 1972; Norton and Davis 1977; Leray et al. 1981) and may reflect increasing stress (Swift 1982; Wakeman and Wohlschlag 1983).

The significant differences in the 0-ppt treatment (control) of the time course studies for both *L. punctatus* and *M. punctulatus* suggest not only a handling response but also the more sensitive nature of these two species as compared with *L. microlophus*. Although Norton and Davis (1977) did not find a handling response in the channel catfish (*Ictalurus punctatus*), Eddy (1981) and Barton and Schreck (1987) indicated profound effects of handling and physical stress on ion and water balance in fishes.

The isosmotic point is approached for all three species between 8 and 9 ppt. However, there were no significant changes in the 48-h plasma osmolality values across salinity treatments in *L. microlophus*. This suggests that the redear sunfish is a strong osmoregulator between 0 and 8 ppt. The significant mean increase and variance observed in plasma osmolality across treatments and the longer acclimation period for both *M. punctulatus* and *L. punctatus*, however, suggest that these two species have more difficulty osmoregulating in increasing salinity. Lutz (1972) has shown that the freshwater perch (*Perca fluviatilis*) can accommodate salinities up to one-third seawater (near isosmotic point) but survived only a few days in one-half seawater. He suggested that ion regulatory mechanisms broke down with increasing plasma ion concentrations. A similar pattern was noticed by Furspan et al. (1984) in the stenohaline freshwater catfishes *Ictalurus nebulosus* and *I. punctatus*. One potential explanation why *L. microlophus* was able to regulate consistently across salinity treatments could be a reduction in the amount and location of blood flow through the gills (Nordlie and Leffler 1975). Blood flow through the gills can take different paths which differ in resistance to osmotic flow and oxygen exchange (Hughes and Morgan 1973). Therefore, as the osmotic gradient is being reduced, it could be advantageous for redear sunfish to shunt blood to more resistant paths (filaments) to prevent excessive exposure of blood to the sites of ion and water exchange. This could have led to less variation in osmolality and hematocrit across salinity treatments.

Because *L. punctatus* and *M. punctulatus* have longer "crisis" periods and more variation in osmolality and hematocrit with increasing salinities, it follows that these two species require more energy for osmoregulation. Leray et al. (1981) indicated that additional energy requirements for osmoregulation are needed mainly during the "crisis" period of acclimation. Diurnal tides are a common feature along the Gulf coast of the United States and these 12-h changes in salinity along the tidal river are shorter than the "crisis" period of acclimation for both *L. punctatus* and *M. punctulatus*. Thus, these two species could be in a continual acclimation state, resulting in increased energy consumption.

The significant differences observed in fish sizes within salinity and time treatments or between species are probably not an important factor in explaining the osmoregulatory variation. Although small fishes have a higher metabolic rate and osmoregulation burden than large fishes (Eccles 1985), these determinations generally compare juvenile and adult fishes. In the present study, all fishes were small, and although a 3- or 4-cm size difference can be statistically significant, it is doubtful if any biological or physiological significance can be attached to such minor size variations when all individuals were immature.

In summary, the penetration of low-salinity marsh systems by centrarchids is in part tempered by the ability to acclimate to increasing salinity and tolerate increasing osmotic pressures with a concomitant reduction in hematocrit. Nordlie (1985), reviewing literature on euryhaline cyprinodontids, suggested that the species with the widest salinity tolerance are the best osmoregulators. In the marshes examined in this study, *L. microlophus* was found in the highest salinity environments, supporting experimental evidence that it is the best osmoregulator of the centrarchids examined. Lutz (1972) and Norton and Davis (1977) suggested that the major limiting factors to the survival of freshwater fish in seawater are the absence of efficient branchial and renal mechanisms that can readily adjust to hyperionic media; thus, osmotic pressure increases and cell function deteriorates. The experimental salinity conditions in this study approached the isosmotic point for these centrarchids, and a further increase in the salinity would cause a potentially greater energetic drain for *L. punctatus* and *M. punctulatus*, and thus may in part account for their reduced tolerance of high-salinity habitats.

Acknowledgements

This paper is based in part on a dissertation submitted in partial fulfullment of the Ph.D. requirements at the University of Southern Mississippi. I would like to thank D. E. Gustafson, Jr., T. Aartila, T. Rogge, and J. Knight for their assistance in field work. Nancy Brown-Peterson, S. T. Ross, F. R. Moore, G. Anderson, F. G. Howell, and R. S. Prezant kindly reviewed an earlier version of this manuscript and made many helpful comments. Support was provided by the Department of Biological Sciences, University of Southern Mississippi, and predoctoral fellowships from the Slocum-Lunz Foundation, Inc. and the Mississippi-Alabama Sea-Grant Consortium (NA85AA-D-SG005).

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Estimating Total Fish Abundance and Total Habitat Area in Small Streams Based on Visual Estimation Methods

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Hankin, D. G., and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Can. J. Fish. Aquat. Sci. 45: 834–844.

We present sampling designs for estimating total areas of habitat types and total fish numbers in small streams. Designs are applied independently within strata constructed on the basis of habitat unit type and stream reach. Visual methods for estimating habitat areas and fish numbers are used to increase sample sizes and thereby reduce errors of estimation. Visual estimates of area are made for all habitat units, and visual estimates of fish numbers are made for systematic samples of units within given habitat types. Use of systematic sampling circumvents the requirement for a preexisting map of habitat unit locations and simplifies selection of units. We adjust for possible proportional bias of visual estimation methods by calibrating visual estimates against more accurate estimates made in subsamples of those units for which visual estimates are made. In a test application of these sampling designs, correlations between visual estimates and more accurate estimates were generally high, $r > 0.90$. Calculated 95% confidence bounds on errors of estimation were 13 and 16% for total areas of pools and riffles, respectively, and were 17 and 22% for total numbers of 1+ steelhead trout (*Salmo gairdneri*) and juvenile coho salmon (*Oncorhynchus kisutch*), respectively. Our methods appear to offer a cost-effective alternative to more traditional methods for estimating fish abundance in small streams. In addition, visual estimation surveys can produce detailed maps of the areas and locations of all stream habitat units.

Les auteurs présentent des protocoles d'échantillonnage pour l'estimation de la superficie totale de types d'habitats et du nombre total de poissons de petits cours d'eau. Les protocoles sont appliqués indépendamment à l'intérieur de strates déterminées à partir du type unitaire des habitats et de la section des cours d'eau. Des méthodes visuelles d'estimation de la superficie des habitats et du nombre de poissons sont utilisées afin d'accroître la taille des échantillons et, ainsi, de réduire les erreurs d'estimation. Des estimations visuelles de superficie sont réalisées pour toutes les unités d'habitat et d'autres portent sur le nombre de poissons se trouvant dans des échantillons systématiques d'unités au sein de types d'habitats donnés. L'échantillonnage systématique permet de contourner la nécessité de disposer d'une carte précisant les emplacements des unités d'habitat et de simplifier leur choix. Les biais proportionnels éventuels des méthodes d'estimation visuelle sont corrigés par étalonnage à partir d'estimations plus exactes obtenues de sous-échantillons des unités ayant fait l'objet d'estimations visuelles. Les auteurs ont obtenu, au cours d'un essai de mise en application de ces protocoles, des corrélations entre les résultats d'estimations visuelles et ceux d'estimations plus exactes qui s'avéraient généralement élevées ($r > 0{,}90$). Les limites de confiance à 95 % calculées des erreurs d'estimation étaient de 13 et 16 % pour, respectivement, les superficies totales des fosses et des hauts-fonds et de 17 et 22 % pour le nombre total de truites arc-en-ciel (*Salmo gairdneri*) 1+ et de juvéniles de saumons cohos *Oncorhynchus kisutch*). Les méthodes présentées semblent constituer une solution de remplacement rentable aux méthodes plus classiques d'estimation de l'abondance des poissons dans les petits cours d'eau. De plus, les inventaires par estimations visuelles permettent de produire des cartes détaillées des zones étudiées et des emplacements de toutes les unités d'habitat d'un cours d'eau.

Received May 20, 1987
Accepted January 6, 1988
(J9293)

Reçu le 20 mai 1987
Accepté le 6 janvier 1988

Hankin (1984) showed that typical surveys for estimation of fish abundance in small streams are two-stage sampling designs. Errors of estimation arise from two sources: (a) extrapolation from a small number of sampled stream sections to an entire stream and (b) estimation of fish numbers within sampled sections. Hankin (1984) recommended that sampled sections should be made equivalent to natural habitat units and that independent samples should be drawn from within strata constructed on the basis of habitat unit type and location. He then proposed several alternative two-stage sampling designs and compared their performances in several plausible settings.

The most important conclusion of Hankin's research was that errors of estimation of fish numbers *within* selected units (second stage errors) are likely to be small compared with errors that arise due to variation in fish numbers or densities *between* sampled units (first stage errors). There are a variety of methods whereby first stage errors can be reduced through choice of sampling design. When fish numbers within habitat units are poorly correlated with auxiliary variables such as habitat unit size, however, errors of estimation can be substantially reduced only by increasing the number of sampled habitat units (increasing the first stage sampling fraction).

Budget limitations may rule out a large first stage sampling fraction if costly and time-consuming electrofishing/removal methods or mark–recapture methods are used to estimate numbers of fish within selected units. An alternative to these methods is visual estimation based on independent counts of fish by divers. Although visual estimates of abundance may be less accurate than those obtained using other methods, the average time and expense required to sample a given unit may be much less than for other methods so that the first stage sampling fraction may be substantially increased for a fixed total survey cost.

Diver counts have been previously used to assess fish abundance, principally in larger streams and rivers (Northcote and Wilkie 1963; Schill and Griffith 1984; Gardiner 1984; Hicks and Watson 1985). Reported variation between visual estimates of abundance by independent divers has been small (Northcote and Wilkie 1963; Schill and Griffith 1984), indicating that visual estimates may often be precise (have small variance). Bias of visual estimates has rarely been determined, however, usually because there has been no suitable method for making an extremely accurate estimate with which to judge bias of visual estimates. Northcote and Wilkie (1963) found that divers undercounted the number of fish actually present and that degree of negative bias appeared species dependent. (True numbers of fish present were determined by poisoning.) Diver counts may thus be quite precise but, because they are not unbiased, their use requires correction for bias in estimators for abundance and error of estimation.

The feasibility and accuracy of visual methods for estimation of fish abundance in small streams have not been previously assessed in the fisheries literature. One advantage of working in small streams is that more accurate population estimates can be made using alternative methods of estimation (such as removal or mark–recapture methods). If these more accurate methods generate estimates with very small errors, then these estimates may be assumed equal to the "true" numbers and they may be compared with diver counts to establish bias of visual estimates. If a consistent proportion of those fish actually present are counted (so that proportional bias is nearly constant), then one can calibrate or adjust diver counts by the ratio of true fish numbers to diver counts and obtain an approximately unbiased estimate of the true number of fish present. Errors of estimation of adjusted diver counts may then be calculated based on (a) between-diver variation and (b) the correlation between diver counts and "true" numbers of fish.

In this paper we present practical sampling designs for estimation of fish abundance and total habitat area in small streams based on visual estimation of fish numbers and habitat areas. The effectiveness of these sampling designs depends on the correlations between visual estimates and corresponding true habitat areas and fish numbers. True habitat areas and fish numbers are assessed using more accurate methods of measurement or estimation in a subset of those units in which visual estimates are made. Systematic sampling is used for selection of units, where unit ordering is the natural stream location sequence, thus circumventing the requirement for a preexisting map of habitat units (Hankin 1984) and simplifying selection of sample units.

Results of applications suggest that the increased first stage sampling fraction achievable with diver counts will usually more than compensate for increased errors of estimation within selected units by substantial reduction in first stage variance and in total errors of estimation. When compared with more expensive traditional methods for estimating fish abundance and habitat area, visual estimation methods offer a cost-effective alternative in small streams.

Sampling Designs

In this section we present brief developments of sampling designs and estimators that can be used for estimation of total habitat area and total fish abundance in small streams based on visual estimates. Sampling designs assume that habitat units are first stratified according to habitat type (e.g. riffles, pools, glides) and location (e.g. lower, middle, upper reaches) so as to generate a finite set of habitat type/location strata (e.g. the upper pool stratum; see Hankin 1984). Primary units within strata are of unequal sizes, equivalent to the natural habitat units, and each habitat type/location stratum is sampled independently. Because strata are sampled independently, estimates of fish abundance or habitat area (and their respective estimated variances) can simply be added across strata to give estimates of total fish abundance or habitat area (and estimated variances) for specific habitat types (e.g. total number of fish in all riffles) or for the entire stream (Hankin 1984). In the development that follows, stratum-specific notation has been avoided for simplicity.

Estimation of Total Habitat Area

Visual estimates of habitat areas are made for all habitat units within a given habitat type/location stratum. A systematic (1 in *k*) sample of units is drawn from this stratum and accurate estimates of habitat unit areas are made for each unit appearing in the sample based on uniformly spaced measurements of stream width. We assume that these accurate estimates of habitat area have negligible errors so that they can be equated with the true habitat area.

Definitions

m_i = true area of unit i; $i = 1,2,\ldots,N$
$M = \sum^{N} m_i$ = true total area of all units
x_i = visual estimate of area of unit i
$T_x = \sum^{N} x_i$ = total of visual estimates across all units

It seems reasonable to assume that

(1) $m_i = Qx_i + \epsilon_i; E(\epsilon_i) = 0$

(2) $E(\epsilon_i^2) = x_i\sigma^2.$

Equations (1) and (2) state that the true habitat unit area, m_i, may be regarded as a random variable with expected value Qx_i and variance $x_i\sigma^2$, proportional to the magnitude of the visual estimate of unit area, x_i. They thus incorporate the reasonable notion that possible discrepancies between visual estimates of habitat area and true habitat area will increase as habitat area increases. If these assumptions are met, then the standard ratio estimator is model-unbiased (Cochran 1977, p. 158) and has the form

$$(3)\quad \hat{M} = T_x\hat{Q}$$

where

$$\hat{Q} = \sum^{n} m_i / \sum^{n} x_i$$

with sampling variance approximately estimated from a sample by (Cochran 1977, equation 6.9):

$$(4)\quad \hat{V}(\hat{M}) = \frac{N\,(N-n)}{n\,(n-1)} \sum_{i=1}^{n} (m_i - \hat{Q}x_i)^2.$$

If the model assumptions are not met, then the ratio estimator is not model-unbiased, but bias will be small if the relation between m_i and x_i is linear and passes through the origin.

Estimation of Fish Abundance

Within a given habitat type/location stratum, a systematic sample of n units is selected for which paired independent diver counts of fish numbers are made for each unit in the sample. In a random subsample of these selected units, some more accurate method of estimating fish numbers is also used to allow calibration or adjustment of diver counts and calculation of errors of estimation within selected units. We assume that this more accurate method of estimation has sufficiently small errors that estimates obtained by this method may be regarded as equal to the true numbers of fish actually present in selected units. Estimates of total fish abundance, and estimated variances for these estimates, are calculated based on adjusted diver counts using an estimator appropriate for two-stage sampling designs with equal probability selection of unequal sized primary units (see Hankin 1984).

Definitions

y_i = true number of fish in unit i; $i = 1,2,\ldots,N$

$Y = \sum^{N} y_i$ = true total number of fish in all units

d_{ij} = count of fish by diver j in unit i; $j = 1,2$

$d_i = \sum_{j=1}^{2} d_{ij}/2$ = mean diver count in unit i

n' = number of units for which both diver counts and more accurate estimates of fish numbers are made

n = total number of units for which diver counts are made; $n > n'$

The first step in calculations involves obtaining adjusted estimates of fish numbers within selected units (those that appear in n but do not appear in n') and computing associated within-unit errors of estimation. (For those units that appear in n', the more accurate estimates for y_i should be used.) It seems reasonable to assume that $d_i = y_i$ when $y_i = 0$ (i.e. if no fish are present, then diver counts will be zero) and that diver counts become progressively less reliable as the number of fish present increases. Then, given the above definitions, the true number of fish in habitat unit i can be estimated by

$$(5)\quad \hat{y}_i = d_i\hat{R} \text{ (for } i \text{ not in } n')$$

where

$$\hat{R} = \sum_{i=1}^{n'} y_j \Big/ \sum_{i=1}^{n'} d_i \text{ (for } i \text{ in } n').$$

$\hat{R}$ is a sample-based ratio estimator for R, the true ratio of numbers of fish present to mean counts by divers. $\hat{R}$ will be the best linear unbiased estimator of R if the relationship between y_i and d_i is the same as that specified for m_i and x_i in equations (1) and (2).

Error of estimation of y_i using equation (5) will depend on (a) variation between diver counts within a unit and (b) error of estimation of R. An estimated variance for $\hat{y}_i$, that incorporates both kinds of errors, may be calculated using Goodman's (1960) result for the exact variance of a product of independent random variables (d_i and $\hat{R}$ will be statistically independent for i not in n'):

$$(6)\quad \hat{V}(\hat{y}_i) = \hat{R}^2\hat{V}(d_i) + d_i^2\hat{V}(\hat{R}) - \hat{V}(d_i)\hat{V}(\hat{R}).$$

If between-diver variation ($\hat{V}(d_i)$) is small, then $\hat{V}(\hat{y}_i)$ will be approximately proportional to the square of the mean diver count, a result consistent with the assumption that diver counts become less reliable as the number of fish present increases. If $\hat{V}(d_i)$ is not small, then the first term in equation (6), reflecting between diver variation, may make a substantial contribution to error of estimation.

$\hat{V}(d_i)$ is calculated empirically (Som 1976, p. 30) from between-diver variation as

$$(7)\quad \hat{V}(d_i) = \tfrac{1}{2} \sum_{j=1}^{2} (d_{ij} - d_i)^2$$

and $\hat{V}(\hat{R})$ is calculated using a standard ratio estimation approximation (Cochran 1977, equation 6.13):

$$(8)\quad \hat{V}(\hat{R}) = \frac{(N - n')}{Nn'\,\bar{d}^{\,2}} \sum^{n'} (y_i - \hat{R}d_i)^2/(n'-1)$$

where

$$\bar{d} = \sum^{n'} d_i/n'.$$

Results from equation (7) and (8) are then substituted in equation (6) to generate estimates of errors of estimation within selected units (for i not in n'). If y_i and d_i are highly correlated, then the squared differences between y_i and $\hat{R}d_i$ should be small, so that $\hat{V}(\hat{R})$ will also be small. If, instead, y_i and d_i are poorly correlated, then the squared differences between y_i and $\hat{R}d_i$ will be large so that $\hat{V}(\hat{R})$ will also be large. The form of equation (8) thus points out the importance of consistency in the proportional bias of visual estimates as compared with true numbers of fish present.

The total number of fish within a habitat type/location stratum can now be estimated as

$$(9)\quad \hat{Y} = \frac{N}{n} \sum^{n} \hat{y}_i$$

where n equals the number of units in the systematic sample (drawn from N) for which diver counts are made. Although equation (9) is statistically unbiased only when N/k = n, we recommend its general use even when $N/k \neq n$ (see Appendix). Note that if the y_i are highly correlated with visual estimates of habitat unit areas, x_i, then a two-stage ratio estimator may be preferable to equation (9) (see Hankin 1984, his equations (4) and (6)).

An estimate of the variance of this estimated total can be calculated as (Hankin 1984, his equation (3))

$$(10)\quad \hat{V}(\hat{Y}) = \frac{N\,(N-n)\sum^{n}(\hat{y}_i - \bar{\hat{y}})^2}{n\,(n-1)} + \frac{N\sum^{n}\hat{V}(\hat{y}_i)}{n}$$

where

$$\hat{\bar{y}} = \sum^{n} \hat{y}_i / n.$$

In practice, it may be more practical to estimate the ratio (*R*) of true numbers of fish present to (mean) diver counts based on a random sample of units drawn from several habitat/location strata of the same habitat type. For example, one may be willing to assume that *R* is a constant for *all* pools, or for all pools within upper and middle pool strata. In that case, *N* in equation (8) would refer to the sum of the numbers of pools located in all such strata, and *n′* would refer to the total number of units within these strata for which visual estimates and more accurate estimates of abundance were made. We have followed this practice in the example application presented below.

Assessment of the Relative Performance of Visual Estimation

Equation (10) is a sample-based estimator for the true two-stage sampling variance of $\hat{Y}$ (Hankin 1984, his equation (2)):

$$(11)\quad V(\hat{Y}) = \frac{N\,(N-n)\sum^{N}(y_i - \bar{y})^2}{n\,(N-1)} + \frac{N\sum^{N}V(\hat{y}_i)}{n}$$

$$= \frac{N\,(N-n)}{n}\,S_1^2 + \frac{N\sum^{N}V(y_i)}{n}$$

where

$$S_1^2 = \sum^{N}(y_i - \bar{y})^2/(N-1)$$

and is unaffected by sample size, and $\bar{y} = Y/N$. The true sampling variance of $\hat{Y}$ can thus be separated into two terms. The first term in equation (11) reflects variation between unit totals (first stage variance) and measures error of estimation that arises in single stage sampling (as if the unit totals were all measured without error). The second term reflects an additional contribution to variance due to "subsampling" (estimating y_i) within selected units (second stage variance). Total sampling variance is the sum of the contributions from the two stages of sampling. As the first stage sampling fraction increases, contributions from both the first and second stages of sampling are reduced. In contrast, use of a more accurate method of estimation at the second stage will only reduce the contribution from the second stage.

Raj (1968, p.119) showed that the expected value of the first term in equation (10) equals $V(\hat{Y}) - \sum^{N}V(\hat{y}_i)$, the true total sampling variance of $\hat{Y}$ less the contribution from the second stage when all units are sampled. $\sum^{N}V(\hat{y}_i)$ can therefore be estimated from a sample as the second term in equation (10), and a sample-based estimate of the second term in equation (11) (the contribution from the second stage of sampling) can be obtained as (Murthy 1977, p. 323)

$$(12)\quad \hat{V}_2 = \frac{N^2}{n^2}\sum^{n}\hat{V}(\hat{y}_i).$$

Given $\hat{V}_2$, the contribution from the first stage of sampling (the first term in equation (11)) can be estimated from a sample as $\hat{V}(\hat{Y}) - \hat{V}_2$. Finally, S_1^2 may be estimated as

$$(13)\quad \hat{S}_1^2 = n\,\frac{[\hat{V}(\hat{Y}) - \hat{V}_2]}{N(N-n)}\,.$$

The estimate for S_1^2 from equation (13) can be used to calculate expected sampling variances given alternative first stage sampling fractions, *n/N* (using equation (11) and a sample-based estimate of $\sum^{N}V(\hat{y}_i)$). Based on such calculations, one may compare the expected performances of alternative methods that could be used to estimate fish numbers within selected units. In particular, one may contrast the expected performances of visual estimation methods (with calibration) and more traditional methods such as electrofishing/removal method estimation.

To compare the probable performances of estimators based on visual estimation with those based exclusively on a more accurate method (such as electrofishing), we assumed that the total sampling-related costs of a visual estimation survey could be expressed as

$$(14)\quad C_V = n_V c_V + n_{E|V}\,c_E$$

where n_V is the number of units for which fish abundance is visually estimated, $n_{E|V}$ is the number of units (out of n_V) for which abundance is (also) estimated using a more accurate method (here, electrofishing), and c_V and c_E are the average costs per unit (in man-hours) of estimation using the two methods. If fish abundances were instead estimated using only the more accurate method, then total sampling-related costs would be

$$(15)\quad C_E = n_E\,c_E$$

where $n_E > n_{E|V}$. That is, the number of units in which the more accurate method could be used would be greater (for the same cost) if fish numbers were not visually estimated in additional units.

Because C_E and C_V are expressed in total man-hours, setting $C_V = C_E$ should result in approximately equal total survey costs for visual estimation (with calibration) and for a more accurate estimation method (e.g. electrofishing). Other survey costs (per diem, travel to study site, etc.) should be roughly proportional to the total man-hours expended in survey sampling. For example, let $c_E = 5$ and $c_V = 1$. If fish abundance were visually estimated in 10 units ($n_V = 10$) and were estimated using a more accurate method in 2 units ($n_{E|V} = 2$), then $C_V = (10)(1) + (2)(5) = 20$. Setting $C_E = C_V$ would give $n_E = 4$ if the more accurate method were the only method used to estimate fish abundance. Based on this alternative sample size, expected sampling variance for the more accurate method ($E[V_E(\hat{Y})]$) can be calculated as

$$(16)\quad E[V_E(\hat{Y})] = \frac{N(N-n_E)}{n_E}\,\hat{S}_1^2$$

where *N* is the total number of units in a particular stratum, $\hat{S}_1^2$ is based on sample data for that stratum, and second stage errors of estimation are assumed negligible.

We used equation (13) and collected survey data to estimate a distinct S_1^2 for coho salmon and 1+ steelhead trout in each pool or riffle habitat type/location stratum. Given the total number of units in a particular stratum and the calculated n_E for that stratum, we then calculated an optimistic (i.e. lower than would in practice be achieved) expected total sampling variance for electrofishing ($E[V_E(\hat{Y})]$) using equation (16). This calculation gave an optimistic notion of sampling variance for electrofishing because the solution for n_E was always rounded up, and equation (16) includes no second stage errors. That is, equation (16) assumes that electrofishing would result in (perfect) enumeration of true unit totals.

Finally, we calculated the net relative efficiency (see Hankin 1984) of the visual estimation survey as compared with a survey based exclusively on electrofishing. For each fish species and habitat type/location stratum, net relative efficiencies (NRE) were calculated as

$$(17)\quad \text{NRE (visual electrofishing)} = \frac{E[V_E(\hat{Y})]}{\hat{V}(\hat{Y})} .$$

An Application

Study Site Description

Sampling designs were applied to estimation of habitat areas and abundances of juvenile anadromous salmonids in Cummins Creek, a third-order pristine stream on the central Oregon coast near Yachats. The Cummins Creek basin is 14 km^2 and the stream drains directly into the Pacific Ocean. All work was conducted during July 1985 in the lower 9.6 km of Cummins Creek; a debris jam prevents movement of anadromous salmonids beyond 9.6 km. Flow during the study averaged 0.8m^3/s at the mouth, and water temperatures averaged about 15°C. Stream width ranged from 2 to 16 m and mean depth of individual habitat units ranged from 0.1 to 1.3 m. Gradient averaged 2.5% and exhibited little variation. Stream substrate was cobble with gravel and some sand and small boulders. Debris torrents and beaver dams were common and well-developed side channels and flood terraces occurred throughout the study reach.

Field Survey Methods

Cummins Creek was first stratified into three contiguous reaches (upper, middle, lower) of about the same length based on distribution patterns of juvenile anadromous salmonids (from previous sampling) and large woody debris. The survey began at the mouth and proceeded upstream to the apparent barrier to upstream migration of anadromous salmonids.

Within a given reach, a first team of two individuals classified habitat units as either (1) riffle, (2) pool, (3) glide, or (4) side channel following Bisson et al. (1981). One individual made a visual estimate of the area of each identified habitat unit, and both individuals jointly made accurate measurements of habitat unit areas in systematic samples of 1 out of 10 units in the lower reach and 1 out of 20 units in the middle and upper reaches (for each habitat type, using independent random starts for each habitat type/location stratum). For accurate area measurements, unit widths were measured at 1- or 2-m intervals along the length of the unit and the mean of these measurements was used to estimate mean width. Total unit area was then calculated as the product of unit length times mean width. Estimates of total habitat areas, and estimated variances for these estimates, were calculated for each habitat type/location stratum using equations (3) and (4). Point estimates and variance estimates were then summed across all three reaches to obtain estimates for the entire stream for a particular habitat type.

The first team also marked (with flagging) units in which fish numbers were to be counted by divers approximately 2–5 h later. This delay minimized disturbance to units immediately prior to estimation of fish abundance. Independent counts of fish were made by a team of two divers, using mask and snorkel, for each unit that appeared in a systematic sample of one in five units drawn from each distinct habitat unit type (using independent random starts for each habitat type/location stratum). Divers did not make counts in all units that appeared in these systematic samples, however. Divers occasionally

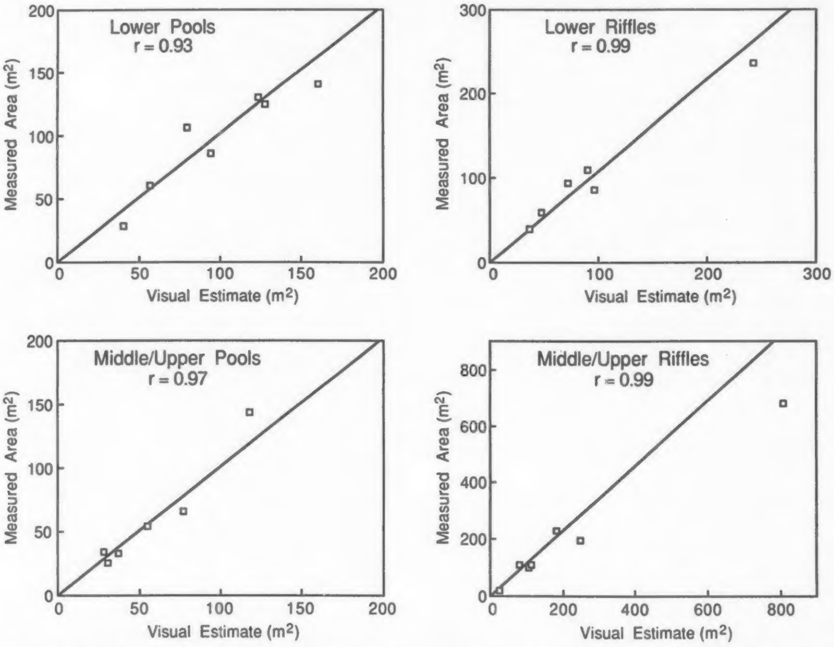

FIG. 1. Plots of accurate measurements against visual estimates of areas for pools and riffles in lower and middle/upper reaches of Cummins Creek in July 1985. Plotted lines are forced through the origin with slopes equal to the estimated ratios of measured areas to visually estimated areas.

TABLE 1. Total number of units (N), number of units accurately measured (n), sample-based estimates of ratios of accurately measured areas to visually estimated areas ($\hat{Q}$), estimated total areas (m^2) of all units ($\hat{M}$), estimated variances for estimated total areas ($\hat{V}(\hat{M})$), and 95% confidence bounds for estimated total areas (95% C.I.) for pools and riffles in lower, middle/upper, and all reaches combined of Cummins Creek in July 1985. Visual estimates of habitat unit areas were made for all units.

Reach	N	n	$\hat{Q}$	$\hat{M}$	$\hat{V}(\hat{M})$	95% C.I.
Pools						
Lower	65	7	0.990	6 141	119 827	±875
Middle/upper	134	6	1.029	8 284	448 315	±1721
All reaches				14 425	568 142	±1938
Riffles						
Lower	62	6	1.066	12 556	159 155	±1026
Middle/upper	124	7	0.926	19 208	3 846 554	±4799
All reaches				31 764	4 005 709	±5146

TABLE 2. Estimated total area (m^2) of all habitat units ($\hat{M}$), unadjusted totals of visual estimates (T_x), total number of habitat units (N), estimated average areas ($\hat{\bar{m}}$), and unadjusted average areas from visual estimates ($\bar{x}$) for pool and riffle habitat type units in lower, middle, and upper reaches of Cummins Creek in July 1985.

Habitat type/ location stratum	N	$\hat{M}$	T_x	$\hat{\bar{m}}$	$\bar{x}$
Lower pools	65	6 141	6 200	94.4	95.4
Middle pools	67	5 925	5 758	88.4	85.9
Upper pools	67	2 358	2 292	35.2	34.2
Lower riffles	62	12 556	11 782	202.5	190.0
Middle riffles	67	11 598	12 525	173.2	187.0
Upper riffles	57	7 670	8 283	134.5	145.3

failed to observe flagging before walking past or through a unit. In all such instances but one, the divers proceeded to the next unit (of a particular habitat type) and made counts in that unit. They then reverted to the original unit sampling sequence. In addition, some selected riffle units in the upper reach of Cummins Creek were very shallow and were extremely difficult to sample by snorkeling. These units were sampled by divers but, because we were unsure of the effectiveness of such efforts, we later electrofished selected areas within these units to verify diver observations. We assumed that these minor departures from true systematic samples did not substantively affect the essential randomness with which sampled units were selected.

Divers entered the water downstream from a selected unit and proceeded slowly upstream, identifying species and/or age-class of fish and counting fish. The two divers positioned themselves near the midline of a selected unit and moved through the unit parallel to one another, using hand signals to coordinate movements. Species and numbers of fish counted were recorded on Plexiglas slates that had surfaces roughened with sandpaper. All observations of fish were made between 0900 and 1600 when visibility was very good, averaging 4–5 m. Species identified and counted included juvenile coho salmon (*Oncorhynchus kisutch*), 0+ and 1+ steelhead trout (*Salmo gairdneri*), and cutthroat trout (*S. clarkii*).

Diver counts were calibrated for each fish species and for each habitat type against a more accurate method of estimation in one out of three pools and riffles (of those snorkled) in the lower and middle reaches and in one out of four pools and riffles (of those snorkled) in the upper reach. These calibration units were a systematic subsample drawn from those units previously snorkled.

As a more accurate method of estimation, we used the Moran–Zippen equal effort (electrofishing) removal method estimator (Seber 1982), applied separately to each species or species/age-class. A five-member team made successive timed removals (passes), using two electrofishing units, in a selected unit until the numbers of fish of each species removed on a particular pass were either zero or less than 10% of those removed during the previous pass. The large size of the electrofishing crew was deemed necessary in order to obtain population estimates with narrow confidence bounds. Many of the sampled units, particularly in the lower and middle reaches, were too large and complex to be sampled effectively with a single electroshocker. Mean numbers of passes per unit were 2.9 for pools (range 2–4) and 2.2 for riffles (range 2–3).

If calculated bounds on errors of estimation of fish abundance based on removal method estimation were $\leqslant 3$ fish for a given unit, then we regarded the estimated number present as sufficiently close to the true number of fish present to warrant use of this datum in calibration of diver counts. If calculated confidence intervals did not meet this criterion, then we omitted such data from those used for calibration. We assumed that the relation established between this more accurate method and diver counts held for all stream reaches for a given habitat type and fish species. We also assumed that those units actually used for calibration constituted an essentially random sample of all units of that habitat type (with respect to the correspondence between diver counts and more accurate estimates).

Diver counts of steelhead trout and coho salmon were often zero in many large upper reach riffles that were difficult to snorkel effectively. To check the validity of these counts, we later electofished many of these units and did not find fish. These units were not included in those used for calibration, however, because their selection was purposive.

Estimated total numbers of fish, by species and/or species/age-class, and variances of these estimates were calculated using equations (5)–(10) for each habitat type/location stratum. Estimates were then summed across all three reaches to generate separate estimates, by species, of the total number of fish in all units of a particular habitat type. Estimates were summed across habitat types to generate estimates of fish abundance, by species, for the entire stream.

Results

We restrict our presentation of survey results to estimation of habitat areas and total abundances of 1+ steelhead trout and coho salmon in the two principal habitat unit types: riffles and pools. Side channels and glides constituted less than 20% of the total number of identified units and less than 5% of the estimated total area of all habitat unit types. Snorkeling was judged not effective for estimation of the numbers of 0+ steelhead trout, and cutthroat trout were present in very small numbers compared with 1+ steelhead trout or coho salmon.

Habitat Areas

Correlations between visually estimated habitat unit areas and accurately measured areas exceeded 0.93 for all riffle and pool habitat/location strata (Fig. 1). Estimated total area of pool habitat was 14 425 m^2, with 95% confidence bounds of ±1938 m^2,

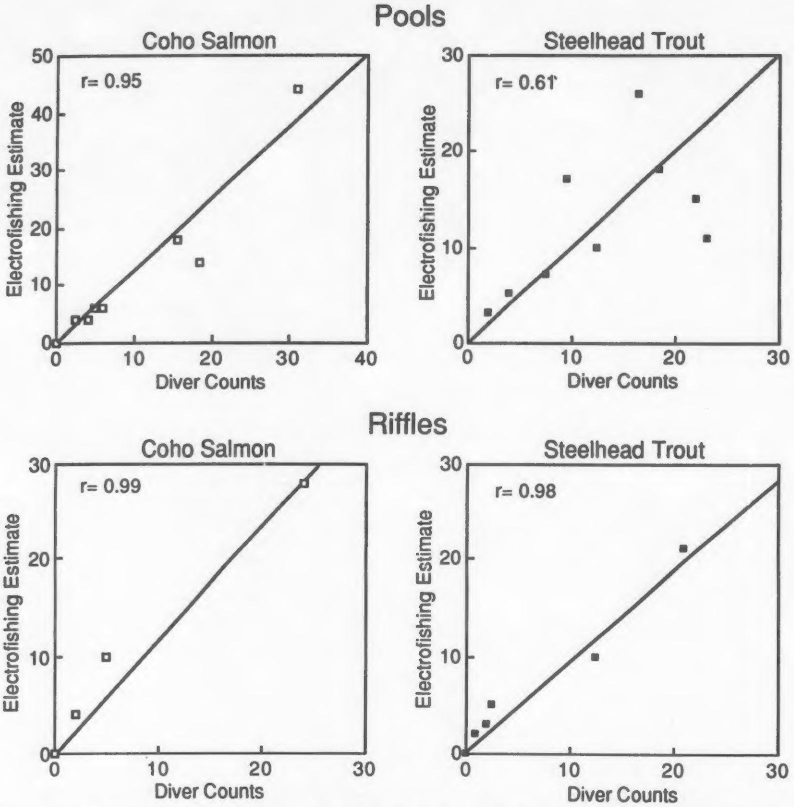

FIG. 2. Plots of numbers of juvenile coho salmon and 1+ steelhead trout estimated present (based on multiple pass removal method estimates) against numbers counted by divers (means of two independent counts) for pools and riffles in Cummins Creek in July 1985. Plotted lines are forced through the origin with slopes equal to the estimated ratios of accurately estimated numbers to visually estimated numbers.

TABLE 3. Independent counts by divers (d_{i1} and d_{i2}) of 1+ steelhead trout in pools in lower, middle, and upper reaches of Cummins Creek in July 1985.

Lower pools		Middle pools		Upper pools	
d_{i1}	d_{i2}	d_{i1}	d_{i2}	d_{i1}	d_{i2}
16	21	6	9	3	3
11	14	5	4	1	1
21	16	33	29	3	3
57	54	21	20	1	1
45	51	23	24	5	7
59	61	17	19	3	2
26	24	8	8	0	0
41	43	8	11	0	0
31	29	15	16	0	0
39	46	19	16	0	0
5	5	13	13	0	0
		4	4	0	0
		10	9		

and estimated total area of riffle habitat was 31 824 m², with 95% confidence bounds of ±5146 m² (Table 1). Confidence bounds were thus from 13 to 16% of estimated total habitat areas. Accurate measurements of habitat unit areas were made in about 7% of the identified pools and riffles.

TABLE 4. Sample correlations between visual estimates of numbers of fish (1+ steelhead trout and juvenile coho salmon) and visual estimates of habitat unit areas for pools and riffles in lower, middle, and upper reaches of Cummins Creek in July 1985. Sample sizes are in parentheses and significant correlations are denoted by superscript "a" ($P < 0.05$) or "b" ($P < 0.01$). No fish were observed in any of the sampled upper riffle habitat units.

Habitat type/ location stratum	Coho salmon (*n*)	Steelhead trout (*n*)
Lower pools	0.420 (11)	0.345 (11)
Middle pools	0.515 (13)	0.177 (13)
Upper pools	0.487 (12)	0.780^b (12)
All pools	0.538^b (36)	0.533^b (36)
Lower riffles	0.419 (10)	0.633^a (10)
Middle riffles	0.108 (13)	0.132 (13)
All riffles	0.206 (32)	0.277 (32)

Average estimated areas of pools and of riffles were similar between lower and middle pool and riffle strata, but average unit sizes were smaller in the upper reach (Table 2). Average area of riffles was about twice that of pools within lower and middle reaches and about four times that of pools within the upper reach.

TABLE 5. Estimated abundances ($\hat{Y}$) of 1+ steelhead trout and juvenile coho salmon, total number of habitat units (N), sample sizes for diver counts (n), and estimated variances of abundance estimates ($\hat{V}(\hat{Y})$) in lower, middle, and upper pools and riffles and in all pools, all riffles, and all pools and riffles in Cummins Creek in July 1985.

Habitat type/ location stratum	N	n	Coho salmon $\hat{Y}$	Coho salmon $\hat{V}(\hat{Y})$	Steelhead trout $\hat{Y}$	Steelhead trout $\hat{V}(\hat{Y})$
Lower pools	65	11	2111	112 769	1480	21 185
Middle pools	67	13	1088	36 024	738	17 205
Upper pools	67	12	101	1 266	428	13 943
All pools			3300	150 059	2646	52 333
Lower riffles	62	10	576	40 407	527	24 505
Middle riffles	67	13	230	5 588	236	4 967
Upper riffles	57	9	0	0	0	0
All riffles			806	45 995	763	29 472
All pools and riffles			4 106	196 054	3409	81 805

TABLE 6. Estimated mean numbers of fish per habitat unit ($\hat{\bar{Y}}$) and mean densities per unit of habitat area ($\hat{\bar{Y}}/\hat{\bar{X}}$, in fish/m²) for 1+ steelhead trout and juvenile coho salmon in lower, middle, and upper pool and riffles in Cummins Creek in July 1985.

Habitat type/ location stratum	Coho salmon $\hat{\bar{Y}}$	Coho salmon $\hat{\bar{Y}}/\hat{\bar{X}}$	Steelhead trout $\hat{\bar{Y}}$	Steelhead trout $\hat{\bar{Y}}/\hat{\bar{X}}$
Lower pools	32.5	0.344	22.8	0.241
Middle pools	16.2	0.184	11.0	0.125
Upper pools	1.5	0.043	6.4	0.182
Lower riffles	9.3	0.046	8.5	0.042
Middle riffles	3.4	0.020	3.5	0.020
Upper riffles	0.0	0.000	0.0	0.000

Calibration of Diver Counts

Figure 2 portrays data used to calibrate diver counts of steelhead trout and coho salmon in riffles and pools. Correlations between diver counts and exhaustive removal method estimates of abundance exceeded 0.94 for steelhead trout and coho salmon in pools and for coho salmon in riffles, but diver counts and accurate estimates were less highly correlated for steelhead trout in pools ($r = 0.61$). Estimated ratios of fish present to mean diver counts ($\hat{R}$) were 1.010 and 1.355 for coho salmon in pools and riffles, respectively, and 0.970 and 1.051 for steelhead trout. Thus, on average, diver counts were similar to accurate estimates for coho salmon and steelhead trout in pools and steelhead trout in riffles, but were less than accurate estimates of coho salmon in riffles.

Estimates of Total Fish Abundance

Agreement between diver counts was good for most sample units (Table 3); absolute differences between counts rarely exceeded four fish and were no more than two fish for most units. Estimated numbers of coho salmon and steelhead trout were largest in lower and middle pools and lower riffles whereas estimated numbers of fish were relatively small in middle riffles and upper pools. Diver counts were all zero for both species in upper riffles. Variation among estimated numbers of fish between habitat units was large in all habitat/location strata for both species (with the exception of upper riffles), and no clear trends of fish numbers with unit locations within habitat type/location strata were apparent.

TABLE 7. Estimated first and second stage contributions to estimated variances of the estimated total numbers of 1+ steelhead trout and juvenile coho salmon in Cummins Creek in July 1985. Estimated mean squared deviations between primary unit totals are indicated by S_1^2. No 1+ steelhead trout or juvenile coho salmon were found in the upper riffle habitat stratum.

Habitat type/ location stratum	First stage contribution	Second stage contribution	S_1^2
Steelhead trout			
Lower pools	14 720	6465	46.1
Middle pools	14 699	2506	52.8
Upper pools	13 352	591	43.5
Lower riffles	23 699	836	73.4
Middle riffles	4 462	505	16.0
Coho salmon			
Lower pools	104 914	7854	328.8
Middle pools	26 934	9089	87.7
Upper pools	1 237	28	4.0
Lower riffles	39 363	1043	122.1
Middle riffles	5 273	314	20.8

TABLE 8. Calculated net relative efficiencies of visual estimation surveys compared with surveys based exclusively on electro-fishing/removal method estimation for estimation of total numbers of 1+ steelhead trout and juvenile coho salmon in Cummins Creek in July 1985. Visual estimates of fish numbers were zero in the upper riffle stratum for both species.

Habitat type/ location stratum	Net relative efficiencies Coho salmon	Net relative efficiencies Steelhead trout
Lower pools	2.27	1.70
Middle pools	2.02	2.55
Upper pools	3.33	3.29
Lower riffles	2.72	2.69
Middle riffles	3.09	2.68

Estimated numbers of fish present in sampled habitat units were not significantly correlated with habitat unit areas for most habitat type/location strata. For habitat type/location strata where fish numbers and habitat areas were significantly correlated, correlations were relatively low (Table 4) and did not justify use of two-stage ratio estimation (see Hankin 1984).

Table 5 summarizes estimates of total abundance of coho salmon and steelhead trout by habitat type/location stratum. For both coho salmon and steelhead trout, estimated totals for lower pool and lower riffle strata were about twice those for middle pool and middle riffle strata. Within the same stream reach, totals for pools were about 3.5 times the totals for riffles. Estimated total abundance of coho salmon in all pools and all riffles were 3300 and 806, respectively, for a pool and riffle total of 4106. The 95% confidence bound for the pool and riffle total was ±886 fish (±21.6% of the estimated total). Analogous estimates for steelhead trout were 2646 and 763 for all pools and all riffles, respectively, giving an estimated 3409 fish for the pool and riffle total. The 95% confidence bound for the steelhead trout pool and riffle total was ± 572 fish (±16.8% of the estimated total).

The wisdom of stratification by habitat unit type and location was supported by strong differences in average fish densities among habitat type/location strata. Mean estimated densities of fish per unit area were much higher in pools and riffles from the lower and middle reaches than from the upper reach. Densities of fish per unit area in pools were 5–10 times those in riffles within a stream reach for both species (Table 6). Steelhead trout and coho salmon densities were similar within all habitat type/location strata with the exception of upper pools where steelhead trout densities averaged about four times those of coho salmon.

Relative Performance of Visual Estimation Methods

Contributions to estimated variance from the second stage of sampling (reflecting within unit errors of estimation only) were relatively small, in most cases, when compared with contributions from the first stage of sampling (Table 7). The majority of calculations thus supported the a priori contention that errors of estimation of fish numbers within units would be small compared with first stage errors.

From the total number of man-hours expended in various survey activities, we calculated that an average of 0.5 man-hours per unit were expended in visual estimation of fish abundance. Electrofishing/removal method estimation required an average of 10 man-hours per unit. Calculated net relative efficiencies for the visual estimation survey (with calibration) as compared with an electrofishing survey ranged from 1.70 to 3.33 across all species and habitat type/location strata and were at least 2.00 in all situations except for steelhead trout in lower pools (Table 8). The correlation between diver counts and accurate estimates of fish numbers were least strong for steelhead trout in pools.

Discussion

Visual methods proved extremely effective for estimation of habitat areas. Besides providing estimates with narrow 95% confidence bounds (±13–16% of estimated total areas of pools and riffles), survey results allowed construction of detailed maps of the locations and sizes of all habitat units. Such maps could be used to compare habitat unit sizes and/or sequences during different months of the year, or to evaluate the effects of various habitat alterations. We emphasize, however, that accurate estimation of habitat areas requires that a single experienced observer be responsible for all visual estimates. It is unlikely that visual estimates of habitat areas made by inexperienced observers will be highly correlated with accurate measured areas, and it is unlikely that several different experienced observers will share the same proportional bias of visual estimation.

In the Cummins Creek survey, estimated numbers of 1+ steelhead trout and juvenile coho salmon were not highly correlated with habitat unit sizes. More complicated sampling designs based on ratio estimation or unequal probability selection of habitat units would not have been effective in such a context (see Hankin 1984). It is exactly under such circumstances, however, that visual estimation of fish numbers may prove most effective. The total number of habitat units for which fish numbers could be estimated was dramatically increased through use of visual estimation. This increased first stage sampling fraction resulted in substantial reduction in first stage sampling errors and in total errors of estimation. As indicated by calculated net relative efficiencies, this reduction in first stage errors more than compensated for a modest increase in second stage sampling errors.

The potential for a large first stage sampling fraction offered by visual estimation is, of course, to some degree compromised by the requirement that the visual estimates be calibrated against more accurate estimates. The time and expense necessary to apply some highly accurate method in a subsample of those units within which visual estimates are made will necessarily limit the total number of habitat units that can be sampled for estimation of fish numbers. In the absence of such calibration, however, it is impossible to generate estimates of true fish abundance based on counts of fish made visually while snorkeling. The proportional bias of diver counts may vary among individuals in different surveys, and may also depend on survey conditions and habitat characteristics such as flow, depth, cover, turbidity, and water temperature (G. H. Reeves, unpubl. obs.; Gardiner 1984). Even under the most favorable conditions, diver counts by themselves are nothing more than rough indicators of true abundance.

We addressed the requirement for calibration by applying a multiple pass removal method estimator in a subsample of those units within which fish were counted by divers and by using only those removal method estimates that appeared to be highly accurate. This device was not entirely satisfactory because the true number of fish present in these units was not known with certainty and because certain units could not be used for calibration because of unreliable removal method estimates. Also, to obtain minimally adequate sample sizes for calibration, we had to assume that diver counts and true fish numbers were related in the same fashion across all reaches of the stream for a given habitat type. Although this method of calibration was less than ideal, it did provide an objective basis for judging the bias and reliability of diver counts of fish. We welcome any suggestions for alternative methods of calibration.

Correlations between diver counts and accurate estimates of fish abundance were quite high ($r \geq 0.94$), except for steelhead trout in pools ($r = 0.61$). The low correlation for steelhead trout may be attributable to the behavior and microhabitat utilization of juvenile trout in pools. Trout were closely associated with the bottom substrate and were often difficult to see. In contrast, coho salmon were more surface-oriented and were easier to observe, particularly when light intensity was reduced. Hartman (1965) reported similar differences in microhabitat distribution of coho salmon and steelhead trout. Everest and Chapman (1972) also found steelhead trout in pools to be closely associated with the substrate.

The behavioral responses of coho salmon and steelhead trout to the presence of divers also differed. Trout were more skitterish and moved to cover more quickly and frequently than salmon, especially in smaller units. Because of this difference in behavioral response to divers, the protocol used by divers was to scan the bottom immediately upon entering a pool and to count trout before salmon.

The patterns of distribution and abundance of habitat units and fish numbers that we found in Cummins Creek suggest that attempts to assess fish abundance based on so-called ''representative reaches'' are unlikely to provide meaningful notions of true fish abundance. We found substantial changes in size and composition of habitat units and in fish species composition and abundance along the length of this stream. About twice as many fish were found in pools in the lower section of Cummins Creek than in the middle or upper sections. Average fish densities (per unit area) in pools were from 4 to 15 times those in riffles. Essentially no 1+ steelhead trout or juvenile coho salmon were present in riffles in the upper section. Mean pool size was larger and pools made up a greater proportion of total habitat area in the lower section than in the middle and upper sections. These examples suggest that extrapolation from data collected in only one or several "representative" reaches could give a highly biased and very misleading picture of true fish abundance.

These changes in distribution of habitat unit sizes and fish numbers also support our construction of habitat type/location strata. Future abundance surveys could take further advantage of these changes in distribution of habitat unit sizes and fish numbers by allocating sampling effort according to estimates of first stage variation (S_1^2) within different habitat type/location strata. Estimates of S_1^2 for coho salmon and 1+ steelhead trout were 122.1 and 73.4, respectively, in lower riffles, 20.8 and 16.0 in middle riffles, and were both zero in upper riffles (no fish were present). For coho salmon in pools, estimates of S_1^2 were 328.8, 87.7, and 4.0 in lower, middle, and upper pools, respectively. According to rules for optimal (Neyman) allocation in stratified sampling (Cochran 1977, Section 5.5.), sample sizes per habitat type/location stratum should be proportional to the products of the stratum size (number of habitat units) and the square root of S_1^2. Thus, optimal allocation of the Cummins Creek survey would result in selection of a large sample size from the lower reach, an intermediate sample size from the middle reach, and a small sample size from the upper reach. Optimal systematic sampling intervals might be 1 in 3, 1 in 6, and 1 in 12 in lower, middle, and upper reaches, respectively.

We believe that the sampling designs we have presented in this paper will prove practical for estimating fish abundance and habitat areas in many small streams. The success of this kind of sampling design will depend, however, on the experience of field personnel and on accurate bookkeeping during survey activities. Divers must be experienced, and they must have established protocols for communicating with one another and for recording fish numbers by species and/or species/age-class. Individuals responsible for identifying habitat unit types and flagging units for later sampling by divers must maintain accurate independent numbering sequences for each habitat unit type. Any lapse of bookkeeping will result in failure to sample a unit or in sampling a unit that should not appear in a systematic sample. If such errors are frequent rather than rare, they may seriously compromise any valid statistical analysis of collected survey data using formulas presented in this paper. The solid performance of a stream survey based on visual estimation that we report in this paper can only be achieved with experienced divers and with careful attention to the details of bookkeeping.

Acknowledgements

We thank Frank Leone, Thomas Dewberry, Gary Susac, and Rob Hanneman for their assistance in collection of field data.

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Appendix. Some Comments on Our Use of Systematic Sampling

We have proposed the use of systematic selection of habitat units to circumvent the need for a preexisting map of all habitat unit locations, and to simplify selection of units in a practical field setting. Systematic selection of units will outperform simple random selection when there is a linear trend of fish numbers with unit location, and will perform as well as simple random selection when fish numbers are unrelated to habitat unit locations. Systematic selection will perform poorly when there is a regular periodic trend of fish numbers with unit locations, and when the systematic selection interval, k, coincides with such a trend (e.g. see Cochran 1977, Sections 8.6–8.8). We regard the possibility of this last situation as remote in the context of small stream surveys.

When systematic selection of units is used, however, equation (9) will give a statistically unbiased estimate of true total fish numbers only if $N/k = n$ (i.e. N/k gives an integer result), or if a circular systematic selection method is used to ensure that sample size is fixed (Murthy 1977, Section 5.2). In practice, it is unlikely that N/k will give an integer result. Also, the device of circular systematic selection may be impractical in a stream survey context.

A statistically unbiased estimator for the total number of fish within a habitat type/location stratum can be obtained using a simple modification of equation (9) (Murthy 1977, Section 5.1):

$$(9') \quad \hat{Y} = k \sum_{i=1}^{n} \hat{y}_i .$$

Equation (9′) compensates for the fact that, when $N/k \neq n$, the sample size n may take on one of two different values depending on the unit location of the original random start. We have not advocated routine use of this well-known unbiased estimator, however.

We have hesitated to recommend general use of equation (9′) because field experience in application of our proposed sampling designs suggests that one or more units that should appear in a systematic sample may be missed due to bookkeeping or other errors (see An Application). If a unit were missed, then the sum of estimated unit totals for sampled units would differ from the expected total (for a particular systematic sample) by the total for the missed unit. In such a situation, application of equation (9′) would therefore result in a very serious negative bias. If execution of the proposed design were flawless (i.e. no units were missed), however, use of equation (9′) would be preferred to use of equation (9).

Timing of Spawning in Norwegian Atlantic Salmon (*Salmo salar*)

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Heggberget, T. G. 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 45: 845–849.

A hypothesis that thermal regime regulates the timing of spawning in Atlantic salmon (*Salmo salar*) was analysed by correlating time of commencement and peak of spawning in 16 Norwegian streams with temperature, latitude, and stream flow. Only temperature during incubation of the eggs proved to have any statistically significant effect. Since the duration of egg incubation is known to depend on temperature regime (i.e. on degree-days), a similar linking of spawning time to stream temperature allows spawning to occur at a time which will result in hatching of eggs at a specific and presumably optimal time for survival of fry.

L'auteur examine l'hypothèse selon laquelle le régime thermique régulariserait la période de frai chez le saumon de l'Atlantique (*Salmo salar*), en corrélant le moment du début et du pic de ponte dans 16 cours d'eau norvégiens avec la température, la latitude et le débit. Seule la température pendant l'incubation semble avoir un effet statistiquement significatif. On sait que la durée de l'incubation dépend du régime thermique (degrés-jours), et ce lien entre le moment de la ponte et la température fait que le frai se produit à un moment qui permettra aux oeufs d'éclore à un moment particulier qui semble optimal pour la survie des alevins.

Received April 1, 1987
Accepted February 9, 1988
(J9217)

Reçu le 1 avril 1987
Accepté le 9 février 1988

Little is known about the mechanisms regulating the time of optimal emergence of Atlantic salmon (*Salmo salar*) fry. Two principal mechanisms may regulate time of hatch, one being a varying response to temperature which regulates rate of development of eggs during incubation, the other being control of spawning time which could depend on water temperatures during spawning and incubation periods or on response of adults to daylength.

Several studies of salmonids indicate that there are no, or only minor, differences in temperature response between families or populations during embryonic development. No stock adaptations in developmental rates were detected in embryos of chum salmon (*Oncorhynchus keta*) (Beacham and Murray 1986) or in disparate populations of Atlantic salmon (Wallace and Heggberget 1988). This suggests that given a particular thermal regime in a river, time of hatching of salmon eggs in that river depends on the time at which the salmon spawn. This study investigates some of the environmental cues which may regulate the timing of spawning in Atlantic salmon.

Materials and Methods

Data on spawning time were collected from 16 brood stock hatcheries in Norway (Fig. 1), where spawning was conducted artificially. Fish were sampled for degree of ripeness 1–2 mo before spawning peaked. Peak spawning was defined as the period when about 50% of the females were ripe, which normally varied by 5–10 d from one year to another. The dates on which the first and last females matured were also recorded, providing data on the length of spawning periods. Average peak spawning and length of spawning for the population from each hatchery were calculated from data collected over 5–10 yr during 1977–86 (data not available for every year in every river).

In addition to the information from brood stock hatcheries, data on spawning time were obtained from four streams (Alta, Gaula, Driva, and Eira) by an aerial method (Heggberget et al. 1986). This method indicated that natural spawning started slightly earlier than artificial spawning of brood stock fish which were kept in captivity for a period before ripening. In the four streams where data on both natural and artificial spawning times were available, the results were averaged.

The number of streams which could be used in the analysis of effects of environmental variables on spawning time depended on the availability of environmental data in the different streams. Data on water flow were available from only 10 streams. Data on water temperature and flow were obtained from the Norwegian Hydroelectrical Board, and these data were averaged over the 5–10 yr (1976–85) in each stream, depending on availability. Daylength was defined as time from sunrise to sunset, and these data were obtained from appropriate almanac tables (Brahde 1970).

Results

Time of Peak Spawning and Length of Spawning Period

The total length of the spawning period was about 1 mo for most of the salmon populations studied, while peak spawning took place within 5–10 d, with minor variations from one year

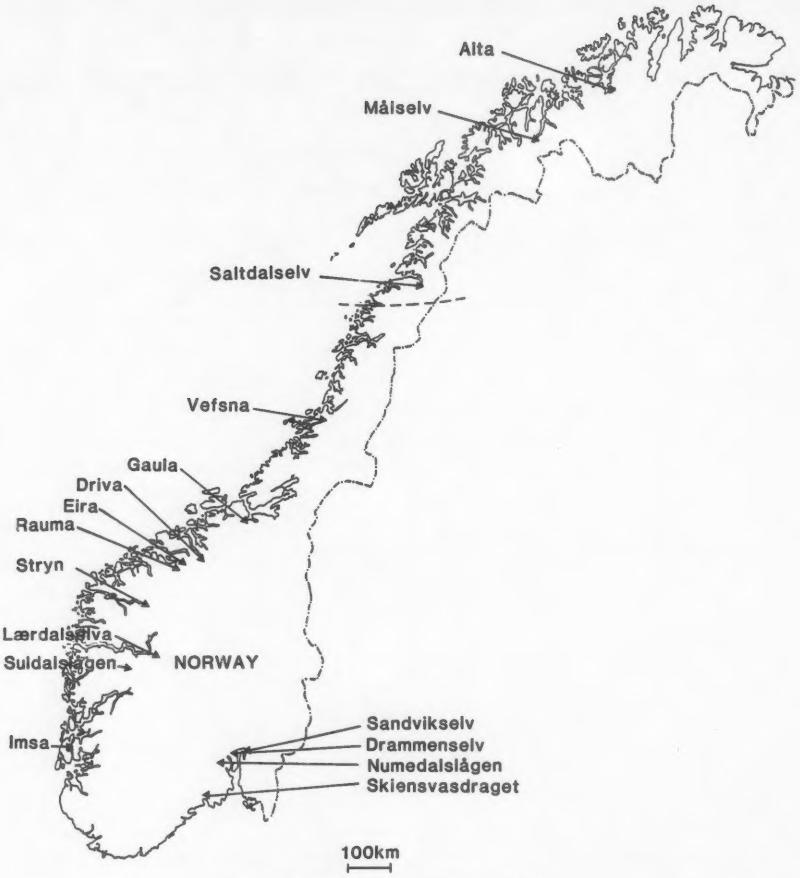

FIG. 1. Location of the streams studied.

to another. The spawning period was more extended in populations which had peak spawning later in the autumn (Fig. 2). Mean length of the spawning period in the 11 early-spawning populations (peak before November 15) was 29.7 d, while mean spawning period in the five late-spawning streams (peak after November 15) was 50.8 d (Table 1, $p < 0.05$, t-test).

Time of Peak Spawning and Latitude

Peak spawning periods for Atlantic salmon in the streams surveyed varied from about October 20 to January 10 (Fig. 2). In the northern streams (63–70°N), peak spawning varied between October 20 and November 5, while in the southern rivers (59–63°N), it varied between October 25 and January 10 (Fig. 2). However, there was no significant correlation between time of spawning and latitude ($r = 0.6099$, df = 14, $p > 0.05$). Because there is no significant correlation between latitude and spawning time, it follows that there is wide variation in daylength at time of spawning between different populations.

Water Temperatures and Spawning

Temperature during peak spawning varied between 1.0 and 4.7°C in the streams studied. Daily mean water temperature decreased during spawning in all streams. Mean temperature wk before peak spawning was 3.3°C, varying between 1.9 and 5.2°C (Table 2) regardless of the latitude of the river. This suggested that water temperature was more important to the timing of spawning than river latitude.

The commencement of spawning (expressed as week No.) was highly positively correlated with mean water temperature for the period December–April ($r = 0.862$, df = 9, $p < 0.001$). In 11 streams for which there were data, spawning time was considerably earlier when mean winter water temperature was low (<1.5°C) than in the streams with higher water temperatures (Fig. 3).

Daylength and Spawning

Daylength varies with latitude, and the streams presently studied are situated at latitudes between 59 and 70°N. Peak spawning took place at daylengths varying from 5 to 9.5 h showing that different salmon populations can spawn at different daylengths.

River Flow and Spawning

No significant correlation between time of spawning and mean time of peak water flow in the incubation period (January–June) was observed for the rivers studied ($r = 0.330$, df $= 14$, $p \leq 0.05$) (Table 3), indicating that water flow is of

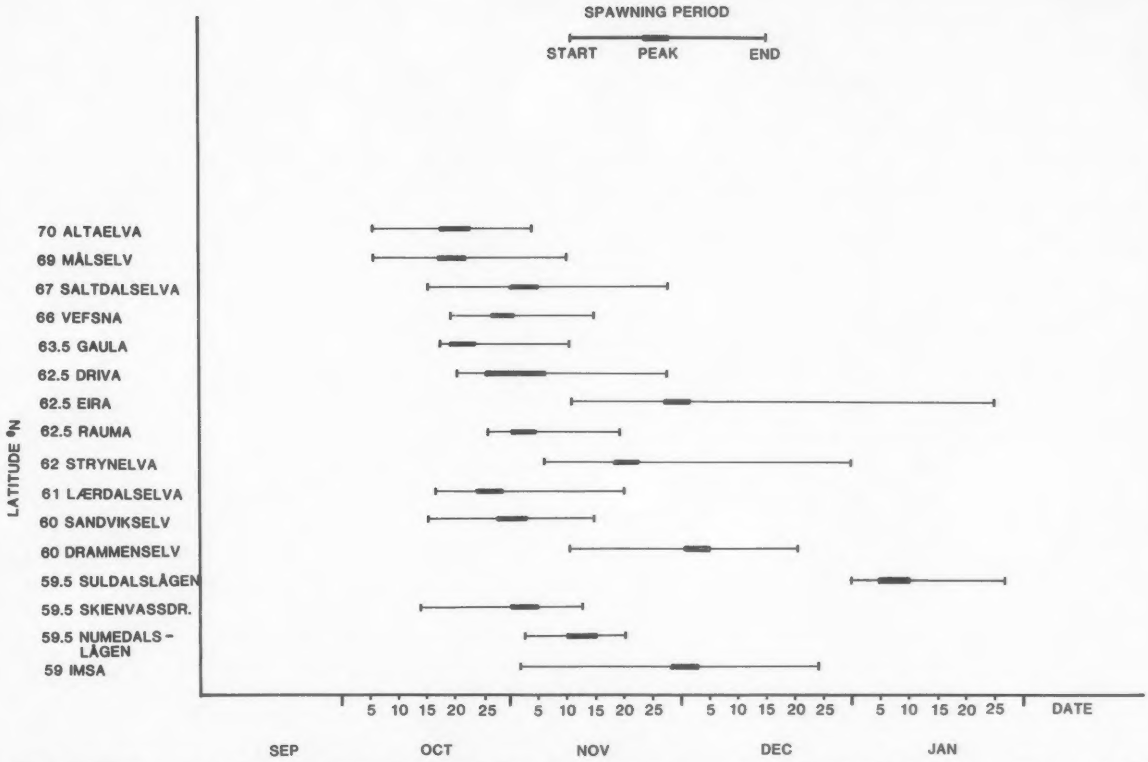

FIG. 2. Spawning time of several Norwegian salmon populations. Peak spawning represents the time when 50% of the females matured. The thick part of the bars represents observed variation of peak spawning.

TABLE 1. Extension of spawning periods in early spawning (before November 15) and late spawning (after November 15) populations of Atlantic salmon.

Peak spawning before November 15	Length of spawning period (d)	Peak spawning after November 15	Length of spawning period (d)
Alta	28	Eira	75
Målselv	35	Strynselv	55
Saltdalselv	43	Suldalslågen	27
Vefsna	26	Imsa	57
Gaula	23	Drammenselva	40
Driva	37		
Rauma	24		
Lærdalselv	34		
Skiensvassdr.	29		
Numedalslågen	18		
Sandvikselv	30		
Mean	29.7		50.8
SD	7.1		18.2

TABLE 2. Water temperature (°C) during spawning for 10 populations of Atlantic salmon.

River	One week before peak spawning	Peak spawning	One week after peak spawning	Mean
Drammenselva	1.9	1.6	1.4	1.63
Numedalslågen	3.0	2.0	0.8	1.93
Imsa	4.7	3.7	3.2	3.87
Strynselv	4.0	3.0	2.8	3.27
Lærdalselv	3.8	2.7	2.5	3.00
Rauma	2.4	1.0	1.0	1.47
Eira	5.2	4.7	4.5	4.80
Suldalslågen	3.3	3.3	3.1	3.23
Vefsna	2.1	1.9	1.5	1.83
Alta	3.1	1.2	0.4	1.57

minor or no importance compared with thermal regime during incubation.

Discussion

The majority of fish species exhibit an annual cycle of reproductive maturation, especially in environments with pronounced seasonally cyclic climates (Bye 1984). In such an environment a fixed spawning time each year coupled with fixed incubation times could ensure a match between larval emergence and presence of food. Photoperiod has been shown to be the major environmental factor in the control of the sequence of endocrine and other physiological changes which ultimately lead to spawning in salmonids (deVlaming 1972; MacQuarrie et al. 1978; Whitehead et al. 1978). If daylength is the predominant cue for timing of spawning, the salmon populations spawning at different lengths of day are adapted to different lengths of photoperiod.

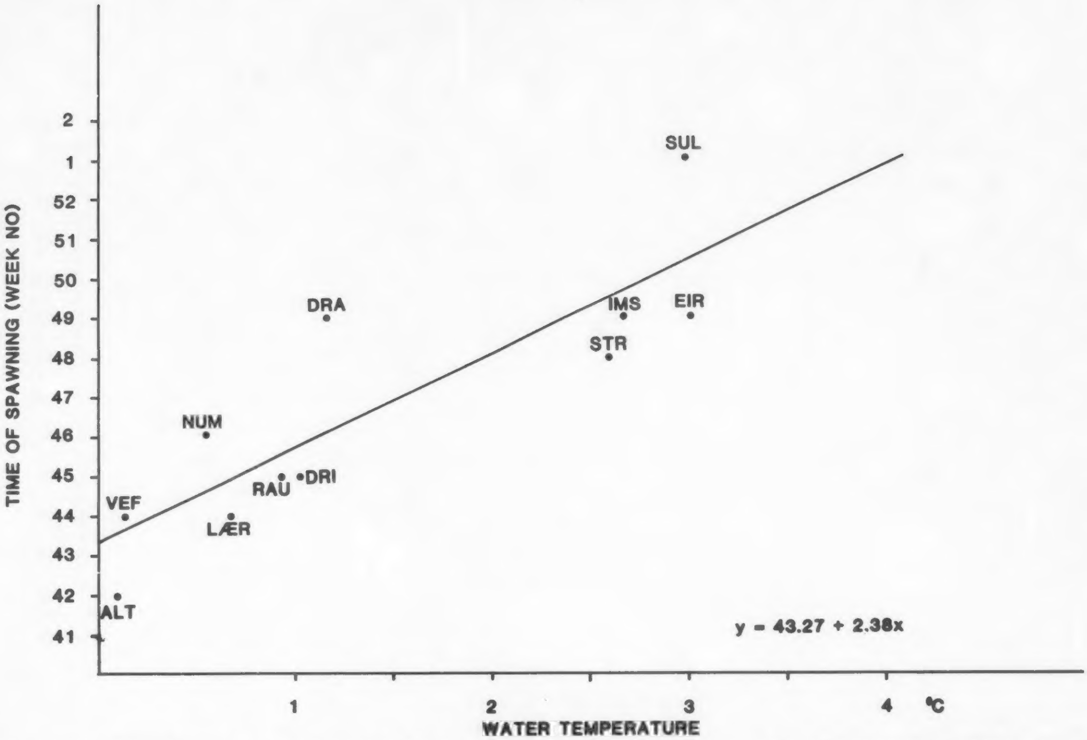

FIG. 3. Spawning time and mean water temperature (°C) in the period December–April. The names of the streams are indicated by the three first letters. For complete name of the streams, see Fig. 1.

TABLE 3. Time of spawning compared with time of peak water flow during incubation.

River	Spawning time (week No.)	Peak water flow (day No.)	SD of peak water flow
Drammenselv	49	147	7
Numedalslågen	46	145	15
Imsa	49	32	30
Lærdalselv	44	158	11
Rauma	45	160	12
Eira	49	160	10
Vefsna	44	149	7
Stryn	48	162	10
Suldalslågen	53	125	53
Alta	42	148	6
Saltdalselv	45	162	13
Driva	45	154	9
Målselv	43	153	10
Gaula	42	141	7
Sandvikselv	45	120	14
Skiensvassdr.	45	140	11

From laboratory experiments, Hamor and Garside (1976) ranked flow rate of water as the primary factor in determining hatching time of eggs of Atlantic salmon. These results are contradictory to the present results, which indicate no correlation between time of spawning and water flow during incubation. The explanation of this discrepancy may be that naturally spawned salmonid eggs are buried 10–20 cm in the gravel (Ottaway et al. 1981) and thus are partly protected from mechanical disturbances. The mechanical effects of water flow on eggs directly exposed to water flowing through an incubation chamber as used by Hamor and Garside (1976) are much more pronounced than for eggs buried in the gravel.

Water temperature during maturation may play a role in determining the time of spawning of salmonids (Henderson 1963; Morrison and Smith 1986). Mean water temperature during peak spawning varied between 1.5 and 4.7°C for the streams included in the present study, showing that spawning occurs at various temperatures in various stocks of Atlantic salmon. In all the streams there was a significant decrease in temperature during the period of spawning. Peterson et al. (1977) reported spawning of Atlantic salmon in the Miramichi River when temperatures were about 6°C and falling, indicating that populations of Atlantic salmon in Norway spawn at colder temperatures than those in Canada.

The results from the present study suggest a causal relation between thermal regime during incubation and time of spawning. Several other studies on spawning time of salmonids support the present results. Burger et al. (1985) in a study of chinook salmon (*Oncorhynchus tshawytscha*) determined that spawning peaked during August in lake-fed tributaries, while spawning peaked during July in tributaries not influenced by lakes. Lakes normally increase autumn and winter temperatures of downstream areas. Sheridan (1962) observed that pink salmon (*Oncorhynchus gorbuscha*) spawned early in cold streams in Alaska and later in warmer streams, the ova thus receiving about the same number of temperature units by the beginning of spring, so that fry in these streams emerge about the same time. In the Eira, Sømme (1954) reported that Atlantic salmon and brown trout (*Salmo trutta*) spawned considerably earlier in the lower part than in the upper part of the river. Eira is lake-fed, and the upper part of the river remains ice-free during most of the winter, while the lower part of the river is colder and has some ice formation. These data indicate a sympatric segregation in time of spawning of Atlantic salmon, which may be attributed to small temperature differences during incubation.

A practical implication of the results is that enhancement programmes involving fish transplantations should take into account the thermal regime of the donor stream. If the relationship between time of spawning and water temperature is genetically controlled or influenced, then the chance of establishing a self-perpetuating population in the stream being enhanced is better if the donor stock comes from a stream with a similar temperature regime. Also, escaped fish from the fast-growing fish farming industry entering Norwegian streams to spawn will have reduced chances of reproductive success if their time of spawning does not match the local thermal regime.

Acknowledgements

The fishery consultants of the County Environmental Departments and several sport fishery organizations are thanked for providing data on spawning. B. Jonsson, T. Beacham, and E. T. Garside are thanked for many suggestions to improve an earlier draft of this manuscript.

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Inseason Forecasting of Bristol Bay, Alaska, Sockeye Salmon (*Oncorhynchus nerka*) Abundance Using Bayesian Probability Theory

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Fried, S. M., and R. Hilborn. 1988. Inseason forecasting of Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*) abundance using Bayesian probability theory. Can. J. Fish. Aquat. Sci. 45: 850–855.

A Bayesian probability model was developed for the Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*) fishery to examine potential benefits of using a formal framework for incorporating several independent run size estimators into a single "best" estimate of total run size. To simulate performance of the technique, a hindcasting procedure was used for the years 1980–87. The Bayesian composite forecast was always more accurate than the least accurate individual forecast and was sometimes more accurate than the most accurate individual forecast. Since forecast accuracy for each independent method varied greatly both among and within years, the Bayesian method avoided the difficult problem of selecting the most accurate individual forecast and allowed forecasts to be easily revised each day of the season as new information became available. The documentation provided by our method should make it easier to evaluate and improve inseason run size estimation procedures and should allow for smoother transitions when management staff changes occur.

Un modèle probabiliste bayésien a été élaboré pour la pêche au saumon nerka (*Oncorhynchus nerka*) à Bristol Bay, en Alaska, afin d'examiner les avantages possibles de l'utilisation d'une structure formelle permettant de produire, à partir de plusieurs estimateurs indépendants de la taille de la remonte, une « meilleure » estimation unique de la taille totale de la remonte. Pour simuler l'efficacité de la technique, on a effectué des prévisions a posteriori pour les années 1980 à 1987. Le degré d'exactitude de la prévision composite produite à l'aide du modèle bayésien était toujours supérieur à celui de la prévision individuelle la moins exacte, et parfois supérieur à celui de la prévision individuelle la plus exacte. Comme l'exactitude des prévisions pour chaque méthode indépendante variait énormément tant entre les années qu'à l'intérieur d'une année, la méthode bayésienne éliminait le problème difficile du choix de la prévision individuelle la plus exacte et permettait de procéder facilement à une révision des prévisions, chaque jour de la saison, à mesure que de nouvelles données devenaient disponibles. La documentation établie à l'aide de notre méthode devrait rendre plus facile l'évaluation et l'amélioration des techniques d'estimation de la taille de la remonte au cours d'une saison et devrait permettre d'aplanir les problèmes de transition lorsque surviennent des changements dans le personnel de gestion.

Received August 8, 1986
Accepted January 11, 1988
(J8899)

Reçu le 8 août 1986
Accepté le 11 janvier 1988

Most North American Pacific coast commercial fishing jurisdictions have highly developed management systems to regulate harvests of Pacific salmon (*Oncorhynchus* sp.) (Walters and Buckingham 1975; Mundy and Mathisen 1981; Wright 1981). The most important element of any inseason management system is the run size estimate, which is needed to determine the number of salmon available for harvest. Run size estimates can be obtained from preseason forecasts, inseason test fishing, commercial catch reporting and spawning escapement monitoring. Managers must then use their experience and intuition to either choose a single indicator or to subjectively weigh and combine several indicators to obtain an estimate of run size. This process often occurs every day of the season as new information becomes available and decisions must be made regarding where and when to allow commercial harvests.

Commercial salmon fishing within Bristol Bay occurs within five fishing districts located near the mouths of major river systems. Under a limited entry system, permits to harvest Pacific salmon within Bristol Bay have been issued to about 1800 drift gillnet and 1000 set gillnet fishermen. Although sockeye salmon (*O. nerka*) are present within these districts from early June through early August, most arrive during a 3- to 4-wk period. On average, only about 1% of the total Bristol Bay sockeye salmon run has been accounted for in the catch and escapement by 22 June (range 0–5%), about 50% by 7 July (range 14–74%), and about 90% by 15 July (range 85–95%).

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Sockeye salmon bound for Bristol Bay spawning systems are also harvested in commercial fisheries in the vicinity of the Shumagin Islands and along the south side of the Alaska Peninsula (hereafter referred to as Unimak) during 1–30 June. Permits to harvest Pacific salmon within this area have been limited to 111 purse-seine, 155 drift gillnet, and 110 set gillnet fishermen. Additionally, the sockeye salmon harvest each season for the Shumagin Island and Unimak fisheries has been set at 1.5 and 6.8%, respectively, of the total number of Bristol Bay sockeye salmon projected to be surplus to spawning escapement and subsistence user needs.

State fishery managers attempt to provide commercial fishermen with adequate opportunities to harvest surplus sockeye salmon. To accomplish this task, managers are provided with a run size forecast several months prior to the fishing season and information on commercial catches, spawning escapements, and test fishing projects during the season. Although inseason data management and analyses have been greatly aided by use of computers (e.g. Yuen 1980), no formal method exists for choosing among or combining the various available run size estimators for decision making.

The purpose of this paper is to demonstrate how several independent indicators of run size can be combined into a single "best" estimate using Bayesian probability theory (e.g. Good 1965; Schmitt 1969; Hoel 1971; Lindley 1971). Bayesian techniques are commonly used in management science and economics (Hines and Montgomery 1980; Anderson et al. 1982), but have seldom been applied to fisheries problems (e.g. Mangel and Beder (1985) used a Bayesian approach in conjunction with more conventional maximum likelihood methodology to develop a general theory for estimating fish stock abundance from search effort data). We think Bayesian probability theory has been overlooked as a valuable Pacific salmon fisheries management tool. Our work demonstrates that such an approach can provide a formal, yet flexible framework for making inseason forecasts of sockeye salmon abundance, an important component of real time management decisions.

Methods

Bayes' Formula

Bayes' formula can be expressed as (e.g. Hoel 1971)

$$P\{R_i|P,U,M,I\} = \frac{L\{R_i|P,U,M,I\}\cdot P\{R_i\}}{\sum_{i=1}^{n}(L\{R_i|P,U,M,I\}\cdot P\{R_j\})}$$

where $P\{H_i|A\}$ = probability of hypothesis H_i being true, after data observation A is obtained (often referred to as the posterior or revised probability (e.g. Anderson et al. 1982)), $P\{H_i\}$ = probability of hypothesis H_i being true, before data observation A is obtained (usually referred to as the prior probability (e.g. Anderson et al. 1982)), and $P\{A|H_i\}$ = probability of data observation A being obtained, given that hypothesis H_i is true.

To apply Bayes' formula, three conditions must be met: (1) a list of alternative hypotheses must be available which encompass all possible outcomes, (2) prior probabilities must be estimated for each alternative hypothesis, and (3) probabilities must be calculated for obtaining subsequent data observations, given that any alternative hypothesis is true.

As an example, consider the following simplified salmon fisheries problem. A fishery manager wishes to know whether the sockeye salmon run size for the coming season will be either (1) less than or equal to the spawning escapement goal (hypothesis 1 = H_1) or (2) greater than the spawning escapement goal (hypothesis 2 = H_2). Information from the past 5 yr indicates that there is only a 30% chance that the run size will be less than or equal to the escapement goal (i.e. prior probabilities are $P\{H_1\} = 0.30$ and $P\{H_2\} = 0.70$). During the season, the manager uses a test fishery to assess run size. However, a decision on whether or not to allow fishing must be made by 15 June. Otherwise, most fishermen will leave the area to participate in another fishery.

From past experience the manager knows that if cumulative test fishing catch is greater than or equal to 100 salmon by 15 June, there is an 80% chance that actual run size will be greater than the escapement goal (i.e. $P\{A|H_1\} = 0.20$ and $P\{A|H_2\} = 0.80$). The manager also knows that if cumulative test fishing catch is less than 100 salmon by this date, there is only a 40% chance that actual run size will be greater than the escapement goal (i.e. $P\{A|H_1\} = 0.60$ and $P\{A|H_2\} = 0.40$). Using Bayes' formula, the manager can update his preseason run size estimate by using the 15 June test fishing data observation.

If cumulative test fishing catch by 15 June is greater than or equal to 100 salmon, the probability of the run being less than or equal to the escapement goal is

$$P\{H_1|A\} = \frac{(0.30)(0.20)}{[(0.30)(0.20) + (0.70)(0.80)]} = 0.10$$

whereas the probability of the run being greater than the escapement goal is

$$P\{H_2|A\} = \frac{(0.70)(0.80)}{[(0.30)(0.20) + (0.70)(0.809)]} = 0.90.$$

However, if cumulative test fishing catch by 15 June is less than 100 salmon, the following run size probabilities would apply:

$$P\{H_1|A\} = \frac{(0.30)(0.60)}{[(0.30)(0.60) + (0.70)(0.40)]} = 0.39$$

$$P\{H_2|A\} = \frac{(0.70)(0.40)}{[(0.30)(0.60) + (0.70)(0.40)]} = 0.61.$$

The above calculations illustrate how Bayesian probability theory can be used to combine a preseason expectation of run size with an inseason forecast, rather than having to choose between the two. For every hypothesis, a new observation is used to modify prior probabilities and thus produce a new set of posterior probabilities. If daily modification of run size estimates is required, it is possible either to use the previous day's posterior probabilities as prior probabilities for the next day's calculations or to continue to use original prior probabilities in all subsequent calculations. We chose to follow the former procedure, since the accuracy of some inseason forecasting methods did not continually improve (and sometimes worsened) over the course of the season.

Bristol Bay Sockeye Salmon Run Size Estimation

For prior probabilities, we chose a set of 67 alternative hypotheses corresponding to total run sizes ranging from 0 to 66 million (using increments of 1 million sockeye salmon). Actual total inshore returns have ranged from 2.4 to 62.4 million for 1956–87 (mean 22.4 million; standard error 15.0 million). Use of the Kolmogorov–Smirnov one-sample goodness of fit test (Sokal and Rohlf 1969) showed that a gamma probability distribution approximated the actual distribution of run sizes observed for these 32 yr much better ($P < 0.001$) than a normal probability distribution ($P < 0.585$). Therefore, a gamma probability distribution function, modified from Hines and Montgomery (1980), was used to calculate the likelihood of obtaining each of the 67 total run sizes such that

$$L\{R_i\} = [(M/V)R_i]^{[(M^2/V)-1]} \exp^{-[(M/V)R_i]}$$

where R_i = total inshore run size i, M = mean run size for past years, and V = variance of run sizes for past years.

To ensure that the sum of all prior probabilities would equal 1, likelihoods of all possible run sizes were converted to actual prior probabilities ($P\{R_i\}$) by dividing each individual likelihood estimate by the sum of all likelihood estimates:

$$P\{R_i\} = \frac{L\{R_i\}}{\sum_{i=1}^{n} L\{R_i\}}$$

where n = number of different run size hypotheses = 67. The run size having the greatest prior probability of being achieved was chosen as the best Prior forecast of run size.

Four run size estimators were used for the present study: (1) a preseason forecast (Preseason), (2) Unimak cumulative commercial catch per unit of effort (Unimak), (3) Port Moller offshore test fishing cumulative catch per unit of effort (Moller), and (4) Bristol Bay cumulative commercial catch and spawning escapement data from all five fishing districts (Inshore). The Preseason forecast, which itself is a composite of results from various regression models using spawner–recruit, sibling, smolt, or Japanese research vessel catch data (see Fried and Yuen (1987) for a detailed description of preseason forecasting procedures), has been available several months prior to the beginning of each season since 1961. Unimak data have been collected every year since 1977, but attempts to forecast Bristol Bay run size from Unimak data were not made until 1984 (D. M. Eggers and A. R. Shaul, Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, AK 99802, unpubl. data). Moller test fishing has been conducted since 1967 (1967–73, 1975–86, and 1987) and has been used as a forecasting tool since 1970 (e.g. Paulus 1971; Mundy and Mathisen 1981; Yuen and Fried 1985). Inshore data for all major river systems have been collected since 1956 (e.g. Yuen and Nelson 1987) and have been used to estimate total run size since at least the 1960's (Royce 1965).

Simple linear regression models were used to generate daily inseason forecasts from these data:

$$Y_{m,d} = \alpha + \beta X_{m,d}$$

where $Y_{m,d}$ = total run size estimated from data source m for day d, α = y-axis intercept, β = slope of regression line, and $X_{m,d}$ = data from data source m for day d (i.e. cumulative Unimak catch per unit of effort, cumulative Moller indices, or cumulative Inshore catch and escapement).

A hindcasting procedure, in which only data prior to the year of interest were used to calculate predictive equations, was used to simulate results for eight years (1980–87), since daily run size forecasts based on these models were not available for past years. Forecasts from the three inseason data sources (Unimak, Moller, and Inshore) were updated daily during the simulation for each year as new information became available. Daily inseason forecasts for each data source were made only if the F-test for the daily regression model was significant at the 95% level and only if the value of the independent variable fell within the range of the data used to build the predictive model. If both conditions were not met, if new data were not available, or if the forecast was less than the actual daily cumulative run size, the most recent previous forecast for that data source which met all the criteria was used as the daily estimate.

To estimate posterior probabilities, we first calculated likelihoods of achieving any run size based on Preseason, Unimak, Moller, or Inshore data. Since all forecasts were based on linear regression models, a normal probability distribution function, modified from Hines and Montgomery (1980), was used to estimate the likelihood of obtaining each of the 67 total run sizes given any of these three data sources:

$$L\{R_i|F_m\} = \exp^{-[(R_i-F_m)^2/2S_m{}^2]}$$

where F_m = forecasted run size based on data source m and S_m = standard error of the forecast based on data source m, a measure of the variability of predicted values of actual run sizes about the true value of the actual run size for a given forecast, calculated as follows (Sokal and Rohlf 1969):

$$S_m = S_{r\cdot m} \sqrt{1 + 1/n + [(F_{m,y}-\bar{F})^2 / \sum_{y=1}^{n}(F_{m,y}-\bar{F})^2]}$$

where $S_{r\cdot m}$ = standard error of regression estimate of past inshore run size r and past forecasted run size based on data source m (i.e. unexplained error), $F_{m,y}$ = forecasted run size based on data source m for year y, and $\bar{F}$ = mean forecasted run size past n years based on data source m.

To determine whether forecasts from each of the four data sources represented independent estimates of sockeye salmon abundance, we examined product moment correlation coefficients (Sokol and Rohlf 1969) calculated between deviations of daily forecasts from actual run sizes. Only eight significant ($P < 0.05$) correlations, all positive, were found: seven between Inshore forecast deviations and either Unimak (deviations correlated for 3 of 31 days examined: 23, 24, and 26 June) or Moller (deviations correlated for 4 of 17 days examined: 22, 25–27 June) forecast deviations and one between Preseason and Unimak forecast deviations (deviations correlated for 1 of 43 days examined: 11 June).

While these results suggested that Inshore forecasts may not have always been independent of either Unimak or Moller forecasts, significant correlations were few in number, confined to a narrow time window (22–27 June), and based on small sample sizes (four to seven years per comparison). Therefore, for the present study, we assumed that each data source produced an independent forecast of sockeye salmon abundance each day of the season. This allowed us to express composite likelihoods ($L\{R_i|P,U,M,I\}$) as the product of their individual likelihoods (Hines and Montgomery 1980):

$$L\{R_i|P,U,M,I\} = \mathrm{L}\{R_i|P\} \cdot L\{R_i|U\} \cdot L\{R_i|M\} \cdot L\{R_i|I\}.$$

To calculate posterior probabilities, each composite run size likelihood was multiplied by the prior probability of achieving that run size and then divided by the sum of all composite likelihood estimates to ensure that the sum of all prior probabilities would equal 1:

$$P\{R_i|P,U,M,I\} = \frac{L\{R_i|P,U,M,I\} \cdot P\{R_i\}}{\sum_{i=1}^{n} (L\{R_i|P,U,M,I\} \cdot P\{R_j\})} .$$

The run size hypothesis associated with the greatest posterior probability was selected as the best Bayesian composite forecast for that day. Run size hypotheses encompassing 40% of the probability distribution on either side of the best Bayesian forecast were used to delineate the approximate 80% confidence interval.

For all eight years examined, Prior forecasts based on M and V values obtained from the preceding 5-yr period were more accurate than those based on M and V values calculated from either the preceding 10-yr period or from all past years. Therefore, 5-yr M and V values were used to generate prior probability distributions for all simulations.

To compare the accuracy of the Bayesian forecast with its component forecasts, mean absolute percent errors (MAPE) were used (Armstrong 1978):

$$\mathrm{MAPE}_{m,d} = 100 \cdot \frac{\left| \left[\sum_{d=1}^{t} (A - F_{m,d}]/A) \right] \right|}{t}$$

where A = actual run size, $F_{m,d}$ = forecasted run size for method m on day d of the time period, and t = number of days within the time period. During the season, forecast performance was examined for six weekly time periods (4–10 June, 11–17 June, 18–24 June, 25 June –1 July, 2–8 July, and 9–15 July).

Forecasts from each of the three inseason data sources could not be made every day for the eight years examined. Unimak forecasts could be made as early as 1 June and were revised every time a harvest occurred until the fishery closed for the year on 1 July. The last valid Unimak forecast made prior to July 1 of any year was used each preceding day until simulations ended 15 July or actual daily cumulative run size exceeded the Unimak forecast. Only Moller data from 12 June to 3 July were used to build daily models, since start and end times for this project have varied considerably in the past. Linear interpolation was used to estimate any missing data within this time period and, due to use of more effective mesh and web type beginning in 1985 (Bue 1986), catch per unit of effort data for 1985 and 1987 were divided in half to make them more comparable with data from past years. The last valid Moller forecast made prior to 4 July was used each preceding day until simulations ended 15 July or actual daily cumulative run size exceeded the Moller forecast. Inshore forecasts were made as early as 14 June and revised daily until 15 July.

Results

The accuracy of Prior, Preseason, Unimak, Moller, and Inshore forecasts varied considerably both among and within years, and no single method consistently outperformed all the others (Table 1). Both forecasts available before the start of the commercial fishing season, Prior and Preseason, performed similarly for the eight years examined. Prior forecasts had lower MAPE values (i.e. were more accurate) than Preseason forecasts three (1987, 1984, 1982) out of eight years and had the same MAPE one year (1985). Similarly, no one method available during the season, Unimak, Moller, and Inshore, was more accurate than all the others every year or every weekly period within the same year. Inshore forecasts did tend to become more accurate as the season progressed, which was expected because final cumulative catch and escapement was the best estimate of total run size, but were usually not more accurate than both the Unimak and Moller forecasts until 25 June or later (six out of eight years: 1987, 1986, 1985, 1982, 1981, and 1980). Fur-

TABLE 1. Mean absolute percent errors (MAPE) for five independent forecasts and the Bayesian composite forecast of numbers of sockeye salmon returning to Bristol Bay, Alaska, 1980–87. Dashes indicate that a forecast for a method could not be made for any of the days within a time period. The smallest MAPE value for each time period is in boldface type.

		During season					
Method	Before season	4–10 June	11–17 June	18–24 June	25 June – 1 July	2–8 July	9–15 July
				1987			
Prior	17.2	17.2	17.2	**17.2**	**17.2**	**17.2**	17.2
Preseason	39.6	39.6	39.6	39.6	39.6	39.6	39.6
Unimak	—	22.2	40.4	50.2	47.7	47.0	—
Moller	—	—	52.8	47.3	19.1	23.9	24.1
Inshore	—	—	64.5	76.2	24.2	15.5	4.5
Bayes	**8.4**	**10.0**	**14.2**	17.8	18.9	17.8	**3.8**
				1986			
Prior	47.7	47.7	47.7	47.7	47.7	47.7	47.7
Preseason	**5.1**	**5.1**	**5.1**	**5.1**	5.1	5.1	5.1
Unimak	—	—	28.5	27.9	36.1	35.7	35.7
Moller	—	—	—	—	—	—	—
Inshore	—	—	63.0	73.3	54.6	27.9	11.7
Bayes	26.6	26.6	14.5	15.7	**4.3**	**3.3**	**2.7**
				1985			
Prior	4.1	**4.1**	**4.1**	**4.1**	**4.1**	**4.1**	**4.1**
Preseason	4.1	**4.1**	**4.1**	**4.1**	**4.1**	**4.1**	**4.1**
Unimak	—	36.5	18.4	9.5	20.0	21.4	21.4
Moller	—	—	26.0	29.7	27.2	—	—
Inshore	—	—	38.5	40.2	45.6	24.2	10.6
Bayes	**1.4**	15.5	8.4	5.3	6.8	7.2	8.8
				1984			
Prior	**7.1**	**7.1**	**7.1**	7.1	7.1	7.1	7.1
Preseason	24.0	24.0	24.0	24.0	24.0	24.0	24.0
Unimak	—	32.0	62.8	49.2	53.7	56.4	56.4
Moller	—	—	47.9	48.6	54.4	—	—
Inshore	—	—	35.0	37.4	7.8	**2.4**	**4.9**
Bayes	19.3	17.9	14.4	**3.8**	**6.4**	4.5	9.3
				1983			
Prior	34.5	34.5	34.5	34.5	34.5	34.5	34.5
Preseason	**27.1**	27.1	27.1	27.1	27.1	27.1	27.1
Unimak	—	**19.0**	**11.9**	**7.0**	**5.5**	**3.7**	**3.7**
Moller	—	—	—	54.7	63.1	65.8	—
Inshore	—	—	—	10.2	21.5	28.7	10.9
Bayes	30.1	21.7	14.8	22.0	26.7	4.2	5.3
				1982			
Prior	**8.6**	**8.6**	8.6	8.6	8.6	8.6	**8.6**
Preseason	56.6	56.6	56.6	56.6	56.6	56.6	56.6
Unimak	—	10.6	45.8	32.5	39.3	41.2	41.2
Moller	—	—	—	**4.3**	13.4	19.9	19.9
Inshore	—	—	**4.7**	7.7	**4.0**	**6.5**	—
Bayes	44.8	31.2	43.5	34.5	20.2	17.6	14.4

TABLE 1. (*Concluded*)

		During season					
Method	Before season	4–10 June	11–17 June	18–24 June	25 June – 1 July	2–8 July	9–15 July
				1981			
Prior	53.5	53.5	53.5	53.5	53.5	53.5	53.5
Preseason	**22.4**	**22.4**	**22.4**	22.4	22.4	22.4	22.4
Unimak	—	33.1	42.6	50.0	50.0	50.0	50.0
Moller	—	—	72.8	60.9	29.4	31.1	—
Inshore	—	—	—	63.2	19.8	16.9	**13.6**
Bayes	30.2	29.0	31.9	**13.7**	**2.6**	**3.7**	15.4
				1980			
Prior	74.4	74.4	74.4	74.4	74.4	74.4	74.4
Preseason	**12.7**	**12.7**	**12.7**	**12.7**	**12.7**	**12.7**	12.7
Unimak	—	—	—	—	—	—	—
Moller	—	—	85.0	78.4	61.1	62.0	—
Inshore	—	—	—	73.6	62.7	18.6	**11.4**
Bayes	34.3	34.3	45.3	51.7	56.7	27.4	22.4

thermore, Inshore forecasts were often less accurate than either the Prior or Preseason forecasts prior to 25 June (six out of eight years: 1987, 1986, 1985, 1984, 1981, and 1980) and sometimes remained less accurate than either of these forecasts throughout the season (1986 and 1985).

The Bayesian composite forecast was always more accurate than the least accurate of its component forecasts (Table 1). It was also sometimes more accurate than the most accurate component forecast when component forecast errors counterbalanced each other (23% of the 56 time periods examined: four time periods in 1987, three in 1986, one in 1985, two in 1984, and three in 1981). However, a great deal of uncertainty still remained in the inseason forecasting process.

Eighty percent confidence intervals for Bayesian composite forecasts were generally quite wide, although they tended to narrow as the season progressed (Table 2). For six years (1981, 1982, 1984–87) the 80% confidence interval included the correct run size hypothesis on 84–100% of the 45 days examined. For the other two years, performance was poor: correct run size hypotheses were included within the 80% confidence interval only during 50% of the days examined in 1983 and were never included with the interval in 1980.

Discussion

The present paper describes an easily applied technique for calculating and updating a weighted composite estimate of sockeye salmon run size from several independent forecasting methods. We first attempted to use Bayesian probability theory to forecast run size using daily Moller data to update prior probabilities based on the Preseason forecast. Various procedures, all developed for use on a desktop microcomputer, were tested during the 1984–87 commercial salmon seasons in Bristol Bay. Results of these field trials led us to make extensive modifications to our initial approach to inseason forecasting, including addition of Unimak and Inshore forecast components and modification of the prior probability distribution. However, a great deal of uncertainty still remained in the process of inseason forecasting of sockeye salmon abundance and highlights the need for a better understanding of factors affecting migration as well as production.

TABLE 2. Approximate 80% confidence limits for Bayesian composite forecasts of numbers (millions) of sockeye salmon returning to Bristol Bay, Alaska, 1980–87.

		During season					
80% C.I. bounds	Before season	7 June	14 June	21 June	28 June	5 July	12 July
			1987: run size = 27				
Upper	32	32	29	26	27	27	32
Lower	18	18	17	16	17	17	22
			1986: run size = 24				
Upper	37	37	32	31	30	30	28
Lower	23	23	20	21	20	20	20
			1985: run size = 36				
Upper	46	40	47	46	44	45	44
Lower	26	24	31	32	32	33	36
			1984: run size = 41				
Upper	43	38	57	49	43	45	50
Lower	23	24	41	35	31	33	40
			1983: run size = 46				
Upper	40	42	51	44	39	53	53
Lower	22	26	33	28	27	39	43
			1982: run size = 22				
Upper	44	37	38	38	33	32	31
Lower	20	10	20	22	19	20	21
			1981: run size = 34				
Upper	36	32	26	37	41	42	45
Lower	12	14	12	21	27	30	35
			1980: run size = 62				
Upper	54	54	42	41	33	58	58
Lower	28	28	24	23	19	40	40

We recognize that many mathematicians will not regard our approach as truly Bayesian, since we did not incorporate actual intuitive (subjective) probabilities within our analyses (see Good 1965, p. 8–11, for a discussion on Bayesians). While we considered this to be outside the scope of our original study, we did try to select a prior probability distribution, based on run size data from the preceding 5 yr, which might simulate a fishery manager's subjective expectation of run size for the coming season. However, we contend that our method is Bayesian, since it treated the estimate of run size as a random variable associated with a prior postulated density function (e.g. Hoel 1971). We may attempt to include Bristol Bay fishery managers' opinions concerning the performance of each independent forecasting method within future versions of our model, but believe that even our relatively simple approach to inseason run size forecasting will greatly assist real time salmon fisheries management.

Our Bristol Bay example illustrated several benefits of using Bayesian probability theory to generate composite forecasts of Pacific salmon run size. First, since the accuracy of each independent method varied considerably among as well as within years, use of a composite forecast offered a distinct advantage over attempting to choose the most accurate forecast from among several independent methods. While the Bayesian composite forecast was not always more accurate than the most accurate individual method forecast, it was always more accurate than the least accurate individual method. Second, our technique allowed run size forecasts to be easily updated during the season as new information became available. Lastly, our method documented an important aspect of the inseason decision making process by placing it within a formal framework. This should enhance our ability to improve inseason forecasting and provide greater continuity within the management process during periods of staff changes.

Acknowledgements

We first began work on the use of Bayes' law for estimating sockeye salmon abundance during a workshop on salmon run forecasting held at the Institute of Animal Resource Ecology, the University of British Columbia, Vancouver, B.C., Canada, in 1984. Since that time our work has profited from the insights and suggestions of Henry J. Yuen, Brian G. Bue, Donald L. Bill, and Charles P. Meacham of the Commercial Fisheries Division within the Alaska Department of Fish and Game. We also thank two anonymous referees of an earlier draft of this paper for their constructive guidance.

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Density-Dependent, Trophic Level Responses to an Introduced Run of Sockeye Salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska

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Sockeye salmon (*Oncorhynchus nerka*) have developed into a major run at Frazer Lake, Kodiak Island, Alaska, reaching over 600 000 adults 34 yr after the first egg-plant in 1951. In the last nine years (1978–86), escapements have averaged over 250 000 with a record high of 486 000 adults in 1985. The increase in escapements were inversely related to seasonal macrozooplankton densities ($p < 0.05$; $r^2 = 0.42$) but directly correlated with increases in the cladoceran to copepod ratio ($p < 0.001$). In addition, the average body length of the smallest macrozooplanker (*Bosmina*) has shifted below the observed threshold length of 0.40 mm for juvenile sockeye prey. We also found an inverse relationship between greater parental escapements and age 1. smolt length ($p < 0.01$; $r^2 = 0.75$). Small-sized smolts produced from a density-dependent rearing environment indicate that spawning capacity equals or exceeds rearing capacity. Juvenile recruits from larger escapements (~400 000) exerted a controlling, density-dependent influence on the secondary trophic level which drastically reduced subsequent adult returns. Moreover, adverse trophic level changes, particularly after the largest escapements, also appeared to reduce the rearing efficiency for lower densities of juveniles, as subsequent smolt sizes from smaller escapements were less than expected. Thus, these findings not only provide a rationale for suggesting that fewer spawners would provide recruits more closely matching the rearing capacity of this lake, but also provide empirical evidence for the potential adverse density-dependent effects of large escapements.

Trente-quatre ans après le premier déversement d'oeufs en 1951, la remonte de saumons nerkas (*Oncorhynchus nerka*) dans le lac Frazer (île Kodiak, Alaska) a atteint une proportion importante et comprend plus de 600 000 adultes. Au cours des neuf dernières années (1978–1986), l'échappée moyenne s'est élevée à plus de 250 000 individus et a atteint un niveau record de 486 000 adultes en 1985. L'augmentation de l'échappée était en relation inverse avec les densités saisonnières de macro-zooplankton ($p < 0,05$; $r^2 = 0,42$), mais était en relation directe avec des augmentations des rapports cladocères-copépodes ($p < 0,001$). De plus, la longueur moyenne du corps du plus petit macro-zooplankton (*Bosmina*) est passée sous la longueur seuil observée de 0,40 mm à titre de proie pour les saumons nerkas juvéniles. On a relevé une relation inverse entre une plus grande échappée des parents et la longueur des smolts 1. ($p < 0,01$; $r^2 = 0,75$). La petite taille des smolts provenant d'un environnement où la croissance était liée à la densité révèle que la capacité de reproduction est égale ou dépasse la capacité de croissance. Le recrutement de juvéniles à partir d'échappées plus importantes (~400 000) a exercé une influence répressive liée à la densité sur le second niveau trophique, ce qui a amené une baisse draconienne du nombre d'adultes amontants. De plus, des variations négatives du niveau trophique, surtout après les plus grandes échappées, semblent avoir réduit l'efficacité de croissance des juvéniles à de plus faibles densités car la taille des smolts issus de plus petites échappées ultérieures était moins élevée que prévue. En plus de suggérer que moins de géniteurs produiraient des recrues plus étroitement associées à la capacité de croissance de ce lac, les résultats obtenus constituent une preuve empirique des incidences négatives potentielles liées à la densité dans le cas d'échappées importantes.

Received April 30, 1987
Accepted January 7, 1988
(J9223)

Reçu le 30 avril 1987
Accepté le 7 janvier 1988

Sockeye salmon (*Oncorhynchus nerka*) eggs were first seeded in the Frazer Lake system in 1951 to establish a self-sustaining population. Although smolts emigrating from the lake could pass over the falls without significant mortality, a steeppass fishway was constructed in 1962 at the 10-m-high falls to allow passage of adult salmon into the lake (Blackett 1979). In 1979, a second fishway was installed parallel to the first to increase salmon entry and passage (Blackett 1987).

The fishway was successful, as Frazer Lake sockeye salmon have developed into a major run on Kodiak Island, necessitating in-season management through use of an escapement goal. As the original sockeye escapement goal was set at ~400 000, most of the returning adults were allowed into the lake to spawn. Since 1978, sockeye escapement has averaged over 250 000, reaching nearly 486 000 sockeye in 1985; however, as escapements neared and exceeded 400 000, smolt sizes and the density of the juvenile forage base (zooplankton) markedly decreased. These changes suggested that increased densities of juvenile sockeye salmon produced from progressively larger escapements were adversely affecting the rearing capacity of Frazer Lake.

Numerous investigators have suggested an inverse relationship between the density of juvenile sockeye salmon in lakes and the rate of juvenile growth (Foerster 1944; Johnson 1961; Krogius 1961; Burgner 1962; Ruggles 1965; Johnson 1965). That is, density-dependent freshwater growth results in a wide range in annual mean smolt sizes (Koenings and Burkett 1987a). Furthermore, Brocksen et al. (1970) used the inverse relationship between biomass of juvenile sockeye and zooplankton from several widely distributed oligotrophic lakes to argue that trophic-level changes result from linkages of density-dependent processes. The purpose of this paper is to illustrate how increasing numbers of sockeye salmon allowed into Frazer Lake, over a period of time, have resulted in marked changes in the plankton community, and the relevence of these changes to assessing escapement levels in sockeye systems exhibiting density-dependent rearing.

Methods and Materials

Description of Study Area

Frazer Lake (57°15′N, 154°10′W) is approximately 15 km long, just under 2 km wide, and is the second largest lake on Kodiak Island, Alaska (Fig. 1). The lake outlet, Frazer River, enters Dog Salmon Creek 4.6 km southwest of the lake which flows 14 km into Olga Bay. The lake is steep-sided, with two major basins, a surface area of 16.6 km^2, a mean depth of 33.2 m, and a volume of 551.1 × 10^6 m^3. The Frazer system is strongly influenced by oceanic climate; if there is an ice cover, it generally thaws by late April. In addition, the mean annual precipitation of 185 cm over a watershed area of 181 km^2 results in an estimated lake water residence time of ~2.1 yr.

The lake is oligotrophic, with a mean May–October total phosphorus (TP) concentration of 4.9 mg/m^3, a total nitrogen (TN) concentration of 135.5 mg/m^3, a TN:TP atom ratio of 60:1, and a seasonal mean chlorophyll *a* concentration of 1.1 mg/m^3. In addition, the lake has a mean euphotic zone depth (compensation point) of 15 m and an euphotic volume of 249 × 10^6 m^3.

Finally, the zooplankton community is composed of two cladocerans (*Bosmina longirostris* and *Daphnia longiremus*), two copepods (*Diaptomus pribilofensis* and *Cyclops columbianus*), and numerous species of rotifers. All five species of Pacific salmon are found in the Frazer Lake system; however, mainly sockeye salmon utilize the nursery area of the lake, as the fishway is closed prior to adult coho salmon (*O. kisutch*) migration. Other resident fish populations include rainbow trout (*Salmo gairdneri*), Dolly Varden char (*Salvelinus malma*), threespine stickleback (*Gasterosteus aculeatus*), and coastrange sculpin (*Cottus aleuticus*).

Limnological Assessment

Lake temperature profiles were obtained with a YSI model 57 temperature meter. Recordings were taken at 1-m increments from the surface to 5 m, at 2-m increments from 6 to 20 m, and at 10-m increments from 20 to 50 m. Beginning in 1985, water quality, nutrient, and chlorophyll *a* levels were determined every 3 wk during June–October after Koenings et al. (1987).

Since 1965, zooplankters at Frazer Lake have been collected using a 0.5-m-diameter, 153-μ-mesh conical net. Replicate vertical tows were taken once each week during May–August at depths ranging from 15 to 55 m at each of four stations (Fig. 1). The net was pulled at a speed of ~1 m/s and washed well before removing and preserving all zooplankton in a 10% buffered formalin solution. Identification and enumeration consisted of withdrawing 1.0-mL aliquots from a known volume with a Hansen-Stemple pipette. Subsamples were placed into a Sedgewick-Rafter cell and all organisms were counted under five 0.01-cm^2 grids using a dissecting microscope. Zooplankton were originally (1965–84) identified to genera and expressed as organisms per cubic metre. However, after detailed limnological surveys began in 1985, zooplankton were identified to species and, in addition, were measured for body length. The length of individual zooplankton was obtained by measuring at least 10 individuals of each species along a transect in each of three 1-mL subsamples to the nearest 0.01 mm, as described by Koenings et al. (1987). Finally, zooplankton populations at both Hidden and Upper Russian lakes used to compare with Frazer Lake were sampled, identified, and enumerated using methods identical to those used at Frazer Lake.

Fish Assessment

Adult sockeye salmon returning to Frazer Lake are counted using two weirs: one located near the mouth of Dog Salmon Creek at Olga Bay and another at the base of the fishway in upper Frazer River. The Dog Salmon weir is used for in-season stock management due to the delayed lag time in migration of salmon reaching the upper Frazer River weir. The weir at upper Frazer River provides more accurate numbers of salmon entering the lake and prespawning mortality (e.g. bear predation). Adult weirs were also operated on Hidden Creek and the Russian River to enumerate adult sockeye returning to Hidden and Upper Russian Lake, respectively.

Since placement of the first fishpass at Frazer Lake in 1962, adult sockeye have been sampled for age, length, weight, and sex data. Sampling schemes varied over the years; however, at least 400 and as many as 2300 adult sockeye salmon were sampled each year from the escapement without known bias. Fish were anesthetized in a tricaine methanesulfonate (MS-222) solution, measured from the mideye to tail fork to the nearest millimetre, and weighed to the nearest 0.1 kg. A scale smear was taken from each fish to determine age composition. The commercial harvest of Frazer Lake sockeye salmon was estimated from escapement counts, migration timing, and district-wide tagging studies used to allocate catches obtained from fish processing tickets.

A weir was operated each spring from 1965 to 1970 to obtain smolt emigration timing, numbers, age, and body size (length and weight) information. However, since 1970, sockeye smolts have been sampled only for index counts, age, and size. Every other day of the migration, 40 smolts were anesthetized in an MS-222 solution, measured from snout to tail fork to the nearest 1.0 mm, and weighed to the nearest 0.1 g. A scale smear was taken from each smolt to determine age.

Population estimates of juvenile sockeye salmon were obtained in 1985 and 1986. In addition, acoustic/trawl surveys

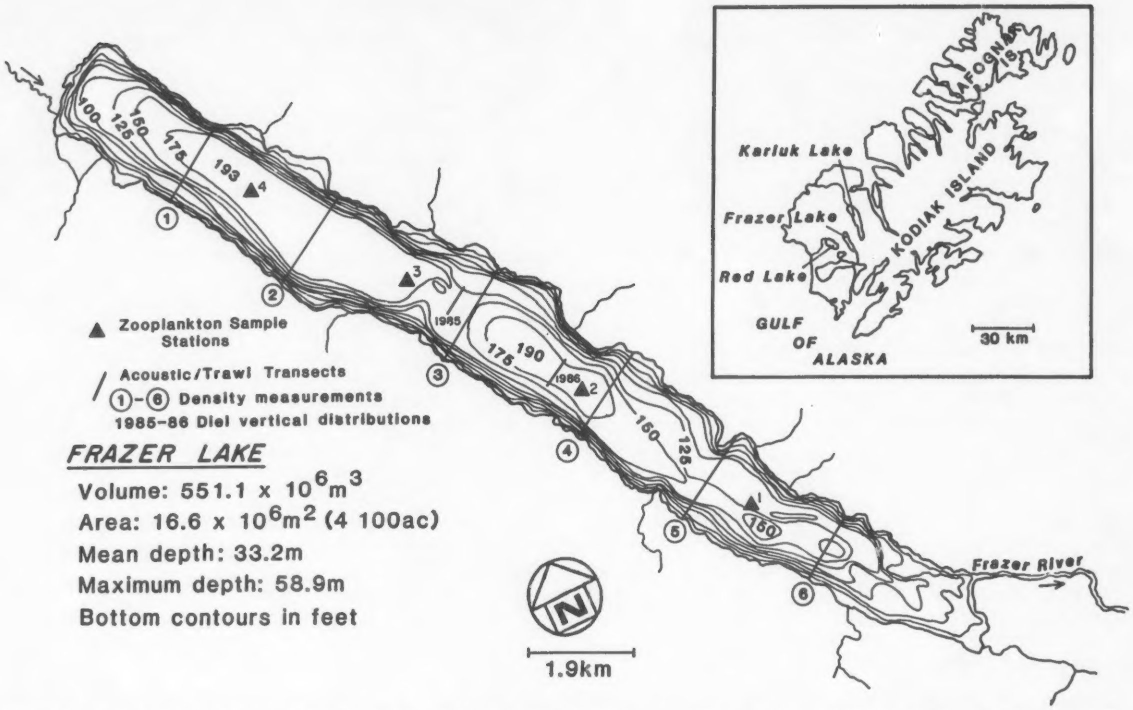

FIG. 1. Morphometric map of Frazer Lake showing zooplankton sampling stations, acoustic transects, and location adjacent to Karluk Lake on Kodiak Island.

were conducted in August 1985 and more intensely in July 1986 to determine the diel vertical distribution of juvenile sockeye salmon. A 20-min paper recording of vertical fish distribution was conducted each year in a midlake location with high fish densities (Fig. 1). On 8 August 1985, vertical fish distributions were recorded at 1200 and 2400; on 11 July 1986, vertical fish distributions were recorded every 6 h for a 24-h period starting at 1800. A Biosonic model 105 single-beam echosounder transmitting a 420-kHz, 100-W pulse of 0.4-ms duration at a rate of 5 pings/s was used for the acoustic surveys. Monitoring and recording of fish signals were accomplished with a Tektronics model 214 oscilloscope, a Biosonic model 115 chart recorder, and a digitized Cannon model VR-30A video cassette recording system. Recorded tapes were analyzed by the University of Washington Fisheries Research Institute for fish densities and resultant population estimates. Moderate fish densities allowed use of echo counting techniques (Saville 1977). Echo counts were made along thirds of six transects (Fig. 1) and in six depth intervals from 2 to 45 m. Total population estimates were obtained by summing fish densities by depth intervals and by extrapolating the lake surface area represented by each transect. Stationary up-looking deployment of the transducer in a midlake location revealed only few fish targets near surface. Consequently, fry population estimates were based on fish densities greater than 2 m in depth.

Open-water trawls were conducted with a 2 × 2 m tow net (Gjernes 1979). Replicated net tows were conducted during darkness in two locations and at depths in which fish signals were the most dense as detected by the acoustic equipment. The entire catch for each tow was preserved in a 10% buffered formalin solution. After at least 6 wk of preservation (to allow for stabilization), fish were measured for length, sampled for age, and analyzed for stomach content. The entire stomach contents of individual juvenile sockeye were identified and enumerated. Zooplankton were sampled from the lake, as previously described, at the same time as the open-water net tows. Zooplankter prey and body size preferred by rearing juvenile sockeye were determined through use of the electivity index (Ivlev 1961).

Results and Discussion

Adult Escapement and Total Return

Total sockeye salmon returns (catch and escapement) to Frazer Lake have dramatically increased over development of the run (Table 1). During the early years (1956–77), adult escapements averaged 32 383, commercial catches (1971–77) averaged 4389, and total returns (1956–77) averaged 33 780 fish. In contrast, during 1978–86, escapements averaged 256 290, while the total return averaged 314 488. The greatest return occurred in 1985 when 131 535 adults were caught and another 485 835 entered the lake, resulting in a total return of 617 370 sockeye. Relatively large commercial catches did not occur until 1978; however, the harvest rate averaged only 19% (58 198) during 1978–86.

The targeted escapement goal of 400 000 was based on (1) estimates of the lake spawning area and the observed spawning area requirement of female spawners (Blackett 1979) and (2) the rearing capacity of Frazer Lake based on rearing depth

TABLE 1. Summary of the Frazer Lake sockeye salmon escapement (1956–86), the estimated commercial catch (1971–86), and the total return. Escapements were recorded at the fishway weir, except during 1956–61 when escapements were recorded at the Dog Salmon weir.

Year	Escapement	Catch estimate	Total return estimate
1956	6	—	6
1957	165	—	165
1958	71	—	71
1959	62	—	62
1960	440	—	440
1961	873	—	873
1962	3 090	—	3 090
1963	11 857	—	11 857
1964	9 966	—	9 966
1965	9 074	—	9 074
1966	16 456	—	16 456
1967	21 834	—	21 834
1968	16 738	—	16 738
1969	14 041	—	14 041
1970	24 039	—	24 039
1971	55 366	10 549	65 915
1972	66 419	2 761	69 180
1973	56 255	1 210	57 465
1974	82 609	2 765	85 374
1975	64 199	3 300	67 499
1976	119 321	8 770	128 091
1977	139 548	1 366	140 914
Mean	32 383	4 389	33 780
1978	141 981	30 336	172 317
1979	126 742	26 805	153 547
1980	405 525	55 173	460 698
1981	377 716	110 210	487 926
1982	430 423	76 232	506 655
1983	158 340	37 983	196 323
1984	53 524	13 853	67 377
1985	485 835	131 535	617 370
1986	126 529	41 652	168 181
Mean	256 290	58 198	314 488

(Russell 1972) and optimum fry planting densities and smolt survivals in nearby lakes on Afognak Island (Meehan 1966; Blackett et al. 1969; Blackett 1979). An average stocking density of 0.15 fry/m^3 produced the maximum number of smolts from these lakes (Blackett 1979). Based on rearing volume, the projected number of sockeye fry Frazer Lake could theoretically support was 60 million. From an assumed egg deposition to fry survival of 10% (Foerster 1968; Drucker 1970; Ellis and McNeil 1979), a measured fecundity of 3000 eggs per female, and an equal sex ratio (Blackett 1979), production of 60 million sockeye fry would require 600 million eggs deposited by 200 000 females. Spawning area capacity was projected to be sufficient for 365 000 viable spawners, while rearing area was estimated to be sufficient to support fry production from 400 000 viable spawners.

As the original escapement goal was set at ~400 000 adults, returning adults of any parent-year during the building of the run remained virtually unfished, and escaped into the lake. Hence, the 30-yr history of Frazer Lake sockeye represents a stock little influenced by direct fishing pressure (Table 1). From 1963 on, we found that age 2.2 adults represented 55% of the returning adults compared with lesser percentages for age 2.3 (21%), 1.2 (16%), and 1.3 (7%) adults. The percentage of age 2.2 adults produced by successive brood-years was linearly related to the total number of brood-year adults (% age 2.2 = $-14\ 810 + 0.551 \times$ total adults; $r^2 = 0.78$).

In addition to the change in the magnitude of the run, the number of adults produced from specific parent-years began to cycle. In particular, the returns of age 2.2 adults showed a 5-yr cycle in abundance that increased in resolution as the run developed (Fig. 2). Low-cycle parent-years occurred in 1963, 1968, 1973, and 1978, while high-cycle years occurred in 1966, 1971, and 1976 and was due to repeat in 1981. However, following the 1978 low-cycle parent-year production of 22 970 age 2.2 adults, production unexpectedly remained at less than 25 000 age 2.2 adults through the entire 1978–82 low/high parent-year cycle, except for the unprecedented production off the 1980 parent-year of 589 393 age 2.2 adults (Table 2). The off-cycle high production of adults from the 1980 parent-year (instead of the 1981 parent-year) resulted from the first escapement that exceeded the original escapement goal of 400 000 (Table 1).

Juvenile Sockeye Densities and the Zooplankton Community

Density-dependent juvenile sockeye salmon growth in Frazer Lake can in part be illustrated by changes in zooplankton densities over the period of increasing adult escapements and by the cumulative effect of high sockeye salmon rearing densities on zooplankter body sizes. For Frazer Lake, we did not have direct measures of juvenile sockeye abundance over time, so we relied on numbers of potential spawners (escapement) through the fishway steeppass in upper Frazer River to provide an index to the abundance of juvenile sockeye salmon rearing in the lake.

During 1965–70, seasonal macrozooplankton (cladoceran and copepod) density averaged 10 620/m^3, while the parent-year sockeye salmon escapement was relatively low (14 684) (Fig. 3A and 3B). For the next 7 parent-years (1970–76), the mean escapement increased almost fivefold to 66 887 adults, while the mean seasonal macrozooplankton density decreased almost threefold to 3590/m^3. More recently (parent-years 1977–86), when escapements dramatically increased (period mean of 257 737), mean seasonal macrozooplankton densities continued to decline averaging only 1450/m^3, an 86% decrease from the 1965–70 period. Moreover, during years when consecutive escapements exceeded 300 000 adults (1980–82), subsequent mean seasonal macrozooplankton densities decreased to as low as 131/m^3 (1981) or by 99% compared with the mean densities of the 1965–70 period. Not surprisingly, a negative logarithmic correlation was found between the parental escapement and subsequent year seasonal macrozooplankton densities ($p <$ 0.05, t-test; $r^2 = 0.42$) over the development of the adult run.

Stenson (1972, 1976) and Kerfoot (1975, 1977) found that when planktivorous salmonids (e.g. sockeye) are abundant, *Bosmina* spp. tend to be of small body sizes. Therefore, we sought evidence of the degree of predation pressure by juvenile sockeye in Frazer Lake from the body sizes of *Bosmina*. Of the 47 juveniles captured in replicated tows in 1985, 37 had either full or moderately full stomachs and none of the individual stomachs was found empty. Similarly, of the 42 juvenile sockeye captured in 1986, 41 had either full or moderately full stomachs and none was found empty. The body sizes of zooplankters found in the stomachs of trawl-caught juvenile sockeye salmon compared with those sampled from Frazer Lake in August of 1985 and 1986 revealed that a continuum of positive electivity indices (active selection) for *Bosmina* existed above the thresh-

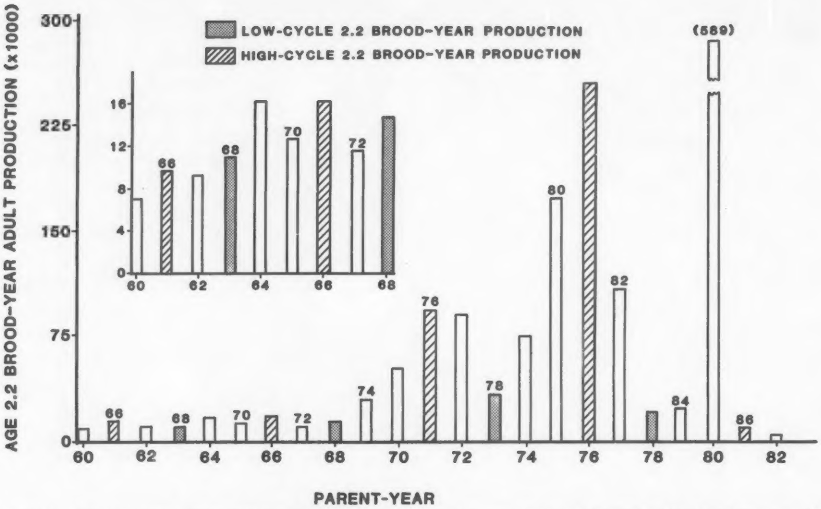

FIG. 2. Age 2.2 brood-year adult production from parent-years 1960–82 showing the development of a high–low 5-yr cycle and its collapse after the 1980 parent-year, when the sockeye escapement in Frazer Lake exceeded 400 000 for the first time. Return years are indicated above each bar.

TABLE 2. Numbers of age 2.2 adults produced from parent-year escapements showing a 5-yr cycle between successive low production brood-years (1963–78) and high production brood-years (1961–76). The anticipated high production brood-year in 1981 was forestalled by the unprecedented production of 589 393 adults in 1980.

Low cycle years						High cycle years			
Parent-year	Age 2.2 adult brood-year production (numbers)	Parent-year	2.2 Age adult brood-year production (numbers)	Parent-year	2.2 Age adult brood-year production (numbers)	Parent-year	Age 2.2 adult brood-year production (numbers)	Parent-year	2.2 Age adult brood-year production (numbers)
—	—	—	—	1960	7 078	1961	9 400	1962	9 170
1963	11 047	1964	16 173	1965	12 519	1966	16 149	1967	11 553
1968	14 998	1969	30 137	1970	51 299	1971	92 226	1972	91 876
1973	31 706	1974	15 084	1975	173 687	1976	257 625	1977	107 918
1978	22 970	1979	24 323	1980	589 393	1981	7 748	1982	3 735

old size of 0.40 mm and for *Daphnia* above the size of ~0.60 mm (Fig. 4). In addition, there were significant differences ($p < 0.0001$, *t*-test) between the body length of *Bosmina* found in juvenile sockeye salmon (mean of 0.43 in August 1985 and 1986) and that found in the lake (mean of 0.32 in August 1985 and 0.34 mm in August 1986) (Table 3). In fact, in most cases (stations and tows), the size of macrozooplankton found in the fry exceeded the sizes found in the lake in August of both years.

The gut contents of Frazer Lake sockeye juveniles agreed with the gut contents of juvenile sockeye salmon collected from different geographical areas in Alaska and Canada (Barraclough and Robinson 1972; Goodlad et al. 1974; G. B. Kyle, Alaska Department of Fish and Game, Soldotna, AK 99669, unpubl. data; Koenings and Burkett 1987a) and from laboratory feeding experiments (J. M. Edmundson, Alaska Department of Fish and Game, Soldotna, AK 99669, pers. comm.) where the smallest macrozooplankton (*Bosmina*) found to be actively selected (positive electivity index) was 0.40 mm in length. Although zooplankton body size measurements were not taken over the years of increasing escapements, the weighted seasonal mean length of *Bosmina* was equal to or less than the size threshold (0.40 mm) in both 1985 and 1986 (Table 3), indicating intense predation pressure by juvenile sockeye.

Excessive planktivory by fish not only reduces prey size, but also structures zooplankton community composition. Brooks (1969) found that *B. longirostris* was dominant in most ponds or lakes in North America and Eurasia where fish predation is intense. He concluded that in zooplankton communities faced with intense planktivore pressure, smaller sized *Bosmina* prevail because they can continue to reproduce at an adult size less than 0.40 mm. Indeed, in recent years at Frazer Lake, *Bosmina* densities were 3–4 times those of the larger sized *Daphnia*. That is, the seasonal mean density of *Bosmina* and *Daphnia* in 1985 was 121 750 and 42 250/m^2, respectively, after rearing 1.9 million (±0.3 million) juvenile sockeye salmon in August. In 1986, seasonal mean densities decreased to 70 890 and 28 950/m^2 for *Bosmina* and *Daphnia*, respectively, after rearing 3.7 million (±0.4 million) juveniles in August. Thus, our recent findings suggest that the reduction in both body size and density of forage preferred by rearing sockeye in Frazer Lake can be linked to the increased recruitment of sockeye salmon fry, which is consistent with the historical trends (Fig. 3).

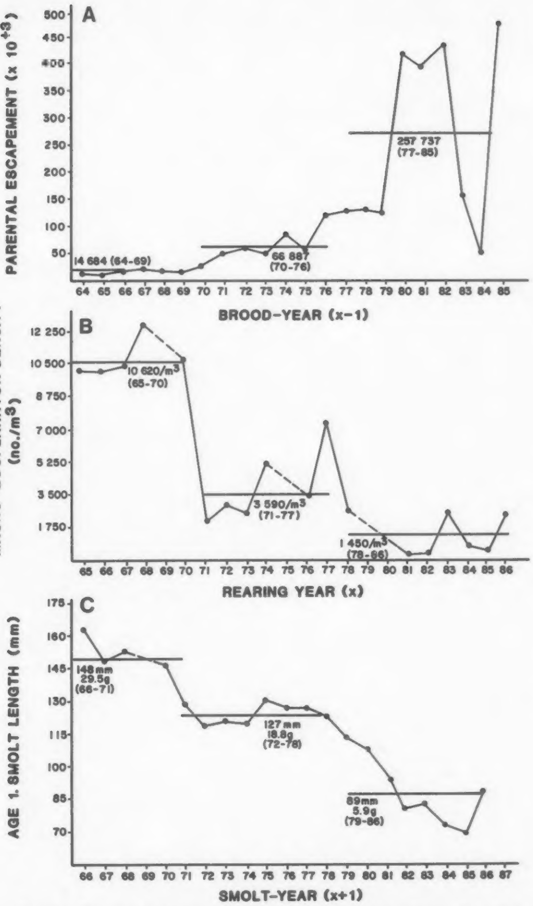

FIG. 3. (A) Parental escapements, (B) macrozooplankton densities, and (C) age 1. smolt sizes during development (1965–86) of sockeye salmon returns to Frazer Lake. Horizontal bars represent average values for three historical periods.

Moreover, the relationship between the magnitude of escapements and both the zooplankton species composition and body sizes is not unique to Frazer Lake. For example, Hidden Lake, located on the Kenai Peninsula, supports a low density of spawners averaging 1500 sockeye/km² (1976–82) and contains the large-sized *Daphnia galeata mendotae* (mean of 1.15 mm) (Fig. 5). In addition, the co-occurring *D. longiremus* and *B. longirostris* were of a larger mean body size in Hidden Lake compared with those in both Frazer Lake (Table 3) with 15 000 spawners/km² (1984–85) and Upper Russian Lake (15 km from Hidden Lake) with an average spawner density of 13 000/km² (1972–84) (Fig. 5). Thus, it appears that in lakes with natural stocks (Upper Russian Lake and Hidden Lake) or introduced stocks (Frazer Lake), those lakes with higher spawner densities lack larger body sized species (e.g. *D. galeata mendotae*) and possess smaller body sizes of *Bosmina* and *Daphnia*.

Adult Escapement and Lake Fertility

Vollenweider (1976, Schindler (1978), and Smith (1979) confirmed the dependence of lake fertility on nutrient loading rates, particularly those of nitrogen (N) and phosphorus (P).

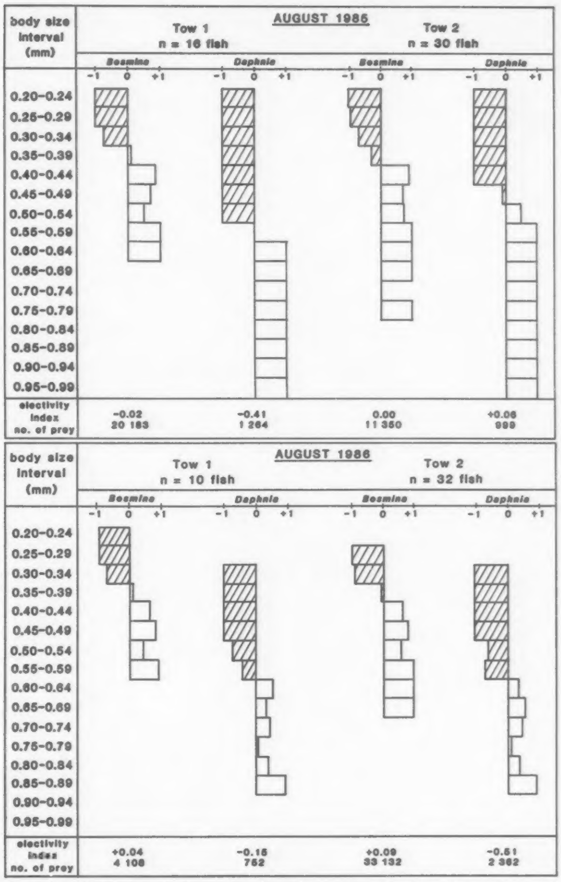

FIG. 4. Electivity indices by length increment for *Bosmina* and *Daphnia* consumed by sockeye salmon juveniles at Frazer Lake during August of 1985 and 1986. Also shown are the number of fish captured/sampled, the number of zooplankton prey consumed, and the overall electivity index for paired net tows 1 and 2.

We estimated an average loading of P from all sources in Frazer Lake during 1985–86 to equal 220 mg P·m⁻²·yr⁻¹. One hundred and seventeen kilograms of P would be added by an average escapement of ~15 000 sockeye carcasses to the Frazer Lake system in early years (1964–69), for an annual surface P loading rate equalling 7.1 mg $P \cdot m^{-2} \cdot yr^{-1}$ (Table 4). During later developmental periods (1970–76 and 1977–86), average escapements equalled ~67 000 and 258 000 fish, with nutrient input increasing to 32.5 and then to 124.2 mg $P \cdot m^{-2} \cdot yr^{-1}$. Higher recent escapements of over 400 000 adults have added an estimated 193 mg $P \cdot m^{-2} \cdot yr^{-1}$, an amount comparable in magnitude with our estimated 1985–86 average P load from all sources. Thus, as escapements of sockeye salmon into Frazer Lake increased, the loading of P theoretically increased by 25-fold, presumably stimulating algal production and the standing stock of herbivorous zooplankters, as suggested for nearby Karluk Lake by Juday et al. (1932) and Koenings and Burkett (1987b).

Sockeye juveniles in Frazer Lake actively selected the herbivorous *Bosmina* and *Daphnia* (Fig. 4) and completely ignored *Cyclops* (very few were found in sampled stomachs), even

TABLE 3. Mean body length by month for *Daphnia* and *Bosmina* at two stations in Frazer Lake during June–October of 1985 and 1986. Also shown are the weighted mean sample lengths from the lake and the mean lengths found in the gut of juvenile sockeye salmon caught in net tows during August of 1985 and 1986.

Station/ zooplankton taxa	Body length (mm)					Seasonal weighted mean (lake)[a]	August mean (fish)
	June	July	Aug.	Sept.	Oct.		
			1985				
Station 1							Tow 1
Bosmina longirostris	0.45	0.39	0.32	0.34	0.40	0.36	0.42
Daphnia longiremus	0.72	0.63	0.56	0.67	0.57	0.59	0.76
Station 3							Tow 2
Bosmina longirostris	0.43	0.39	0.33	0.37	0.37	0.36	0.44
Daphnia longiremus	0.75	0.66	0.76	0.60	0.60	0.61	0.75
			1986				
Station 1							Tow 1
Bosmina longirostris	0.41	0.33	0.34	0.41	0.40	0.40	0.43
Daphnia longiremus	0.65	0.64	0.59	0.55	0.57	0.59	0.69
Station 3							Tow 2
Bosmina longirostris	0.44	0.40	0.34	0.41	0.40	0.40	0.43
Daphnia longiremus	0.75	0.78	0.60	0.60	0.61	0.61	0.72
			1985				
Station 1							
Cyclops columbianus	0.86	0.56	0.68	—	—	0.76	—
Station 3							
Cyclops columbianus	0.73	0.53	0.86	—	—	0.78	—
			1986				
Station 1							
Cyclops columbianus	0.63	—	0.65	—	0.52	0.60	—
Station 3							
Cyclops columbianus	0.74	0.87	0.71	1.11	—	0.83	—

[a]Weighted by number.

though both densities, and particularly body sizes (Table 3), of *Cyclops* and *Daphnia* were comparable. We hypothesize that this occurred because *Cyclops* are more evasive than *Daphnia* (O'Brien 1979; Drenner et al. 1978), and the deep-migrating behavior of *Cyclops* probably overlaps that of ascending juveniles in deeper strata (>15 m) where visual feeding cannot take place. We simply have no evidence suggesting that sockeye juveniles at Frazer Lake selectively forage on *Cyclops*. This is consistent with prior studies at Packers Lake (Koenings and Burkett 1987a), Lake Nunavaugaluk (Jaenicke et al. 1980), and Babine Lake (Narver 1970) and with laboratory studies (Vinyard et al. 1982). Thus, our evidence suggests that *Cyclops* densities at Frazer Lake are not significantly affected by predation from juvenile sockeye salmon. However, during development of the adult run at Frazer Lake, both the density and proportion of *Cyclops* decreased whereas those of the smaller sized zooplankton (*Bosmina*), and particularly the rotifers, increased. As planktivorous fish can selectively reduce preferred prey abundance, and thus structure the zooplankton community of a lake, we questioned why nonprey zooplankters such as *Cyclops* decreased in abundance, while both preferred prey (e.g. *Bosmina*) and nonprey (rotifers) increased in density and relative proportions (Table 4).

We believe that the increase in nutrient loading rates from salmon carcasses in recent years affected food conditions for herbivorous zooplankters and indirectly caused the substantial shifts in the composition of zooplankton at Frazer Lake. That is, during early development of the run (1964–69), escapements averaged only ~15 000 fish, and the average cladoceran to copepod ratio was 0.06 (Table 4). During this time the lake was very oligotrophic, as the zooplankton community was dominated by *Cyclops* and, in all likelihood, by the herbivorous *Diaptomus* (i.e. copepods). Under low food conditions (e.g. low escapements), cladocerans may have been unable to obtain the required energy for successful survival and reproduction because of an inefficient feeding strategy, a phenomenon known to occur in many lake types (Gliwicz 1975, 1986; Allen 1976; Richman and Dodson 1983; Patalis and Salki 1984; Edmundson and Koenings 1986; Koenings et al. 1986).

As enriched lake conditions, caused by increased nutrient (N and P) supply rates (Schindler 1978; Smith 1979), are known to favor the population expansion of herbivorous zooplankters such as *Bosmina*, *Daphnia*, and rotifers (Brooks 1969; Allen 1976; Porter 1977; Gannon and Stemberger 1978; Lampert 1978; Richman and Dodson 1983; Vanni 1986), the import of such quantities of nutrients from salmon carcasses into nursery

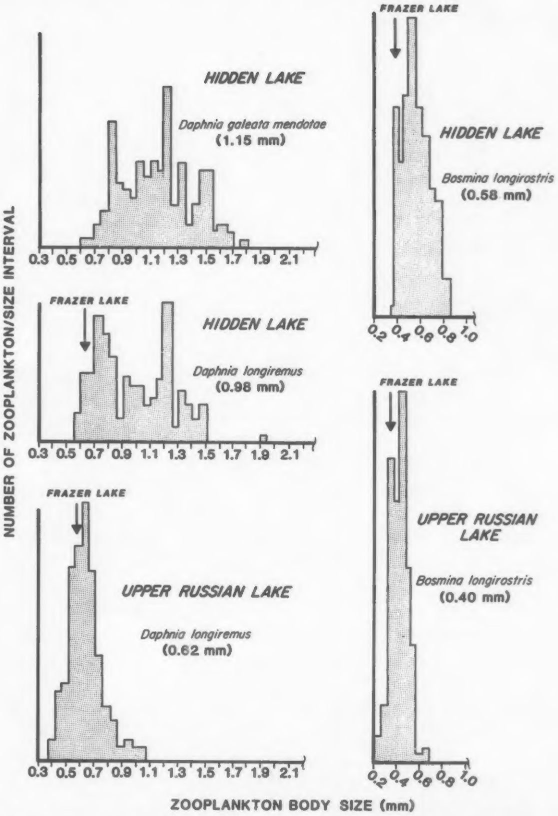

FIG. 5. Frequency of body-size intervals for *Daphnia galeata mendotae, Daphnia longiremis*, and *Bosmina longirostris* during May–October in Upper Russian Lake (13 000 spawners/km^2), Frazer Lake (15 000 spawners/km^2), and Hidden Lake (1500 spawners/km^2). The absence of *Daphnia galeata mendotae* and the presence of smaller size intervals in Upper Russian and Frazer lakes indicate intense predation by rearing sockeye salmon fry.

lakes could substantially enrich the lake and affect food sources for secondary and tertiary production (Mathisen 1972; Koenings and Burkett 1987b). Since *Bosmina* are the only known macrozooplankton capable of matching the rate of increase of microzooplankton (i.e. rotifers) given an increase in food supply (Allen 1976), we would have expected a substantial increase in cladoceran densities with increased fertility. However, during 1965–70, cladocerans comprised 4% of the total zooplankton community, while in later years (1981–86) they represented 15%, a modest but pointed proportional increase of 11%. In contrast, rotifers were unaffected by vertebrate planktivores and were relieved of potential invertebrate predation by the demise of the copepods (i.e. *Cyclops*). As a result, rotifers represented a numerical average of 83% of the total zooplankton community during 1981–86, with a high of 97% in 1982, while during 1965–70 they represented only 23%. It appears that the expected increase in macrozooplankton (e.g. *Bosmina*) was substantially curtailed in recent years due to intense predation by sockeye salmon juveniles. During the 1977–86 period when escapements dramatically increased, the average cladoceran to copepod ratio substantially increased to 8.86 (Table 4). In fact, a significant increase in this ratio was found as escapements increased from <10 000 to average over 250 000 adults ($p < 0.001$, F-test).

Juvenile Growth and Temperature

On the basis of growth and food conversion efficiency, it is generally accepted that rearing temperatures above 5°C but below 15°C are most favorable for young sockeye (Donaldson and Foster 1941; Rounsefell 1958; Brett et al. 1969). However, Koenings and Burkett (1987a) reported that sockeye growth in fertilized Hugh-Smith Lake (a food-satiated rearing environment) was independent of fish density because of a nearly constant mean rearing temperature of 6°C. As Russell (1972) reported finding sockeye fry rearing as deep as 30 m from echo soundings done in 1970, the density-independent effect of low rearing temperature could limit growth. That is, a change in rearing depth could accompany the increased number of juvenile recruits which could account for decreased smolt sizes following the recent larger escapements.

The vertical distribution of juvenile sockeye observed in Frazer Lake during the acoustic surveys done in August 1985 and July 1986 ranged from 3 to 13 m at night and from 16 to 29 m during the day at temperatures of 8.5–11.0 and 7.2–9.5°C, respectively (Fig. 6). Furthermore, considering the calculated heating/cooling regime for the entire growing season in 1985 and 1986, and assuming similar rearing depths (1–20 m) before and after July–August, temperatures were within the acceptable range for favorable growth throughout the rearing season (Table 5). In addition, our results indicate that juvenile sockeye in Frazer Lake exhibit typical diel vertical migration (Narver 1970; Chernoff 1971; McDonald 1973), moving to cooler temperatures presumably for the physiological advantages of a reduced metabolism after feeding in warmer, more productive surface waters. Thus, the growth of juvenile sockeye salmon in Frazer Lake is not inhibited by low rearing temperatures, and may possibly be enhanced by rearing under cyclic temperatures that are neither too low nor high. Therefore, the density of utilizable zooplankton (macrozooplankton) determines the amount and quality of food for rearing juvenile sockeye salmon, and correspondingly that the growth of fry in Frazer Lake is indeed density dependent.

Adult Escapement and Smolt Size

Ample evidence exists from empirical data suggestive of an inverse relationship between juvenile sockeye salmon densities and growth (Foerster 1944; Johnson 1965; Krogius 1961; Burgner 1962; Ruggles 1965; Rogers 1973; Goodlad et al. 1974). Furthermore, progressively greater numbers of juvenile sockeye salmon released in Leisure Lake, a system with an outlet barrier located in coastal southcentral Alaska, resulted in annual decreases in smolt lengths and weights (Koenings and Burkett 1987a). At Frazer Lake during 1964–69, age 1. smolt size averaged 148 mm in length and 29.5 g in weight (Fig. 3C; Table 4), with a high of 163 mm in length in 1966 and 36.3 g in weight in 1968. During the next 7 yr (1970–76), age 1. smolts averaged 127 mm and 18.8 g. In the last 9 yr, through 1986, age 1. smolt size decreased the most of the three periods, averaging 89 mm in length and 5.9 g in weight. We found that during 1978–84 when escapements were very large (Fig. 3A; Table 1), subsequent age 1. smolt sizes decreased to as low as 70 mm in length (Fig. 3C) and 2.6 g in weight. Considering the minimal size for smolting at 60 mm and 2 g (Koenings and Burkett 1987a), the historical change in smolt size represents a 90% reduction

TABLE 4. Changes in zooplankton density and taxa ratio, *P* nutrient loading, and age 1. sockeye smolt sizes with increases in adult sockeye escapements since 1964 at Frazer Lake.

Historical period	Mean sockeye escapement	Zooplankton (no./m^3)[a] Macro	Total	Cladoceran to copepod ratio	Smolt sizes g	mm	Carcass P kg	mg·m^{-2}·yr^{-1}	mg/m^3
Early (1964–69)	14 684	10 620	14 110	0.06	29.5	148	117	7.1	0.21
Middle (1970–76)	66 887	3 590	6 996	0.17	18.8	127	539	32.5	0.96
Late (1977–86)	257 737	1 450	6 907	8.86	5.9	89	2062	124.2	3.62

[a] Total zooplankton refers to cladocerans, copepods, and rotifers whereas macrozooplankton refers to only cladocerans and copepods.

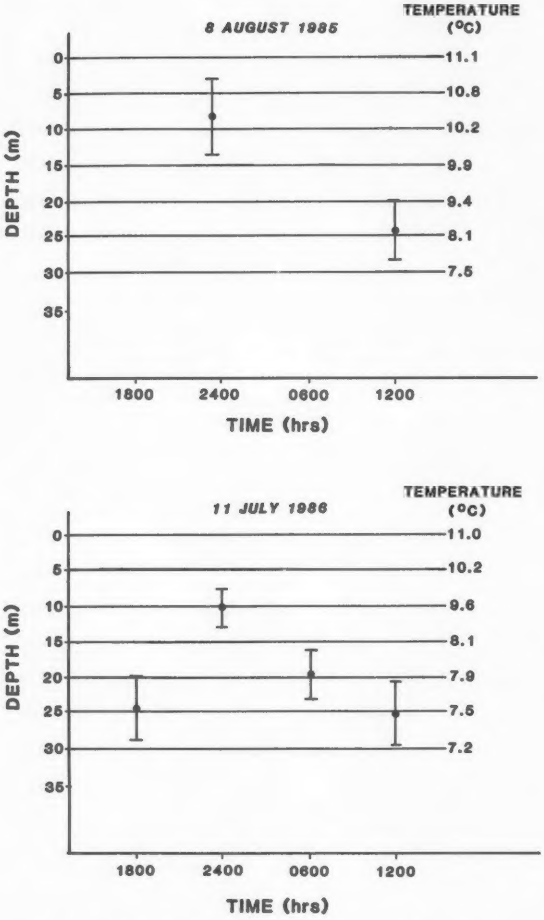

FIG. 6. Rearing depth and temperature for juvenile sockeye salmon in Frazer Lake determined hydroacoustically from day–night (August 1985) and diel (July 1986) monitoring. Points represent the middle depth band of rearing juveniles and the bars depict the upper and lower depths of rearing juveniles.

in length and a 98% reduction in weight. Thus, as escapements increased from a mean of 15 000 during 1964–69 to average over 250 000 during 1978–86, resulting age 1. smolt size decreased in a density-dependent fashion and approached minimal or "threshold" size for smolting.

Despite the density-dependent, trophic level changes (Fig. 3), a positive ($r^2 = 0.19$) but nonsignificant ($p < 0.40$) relationship was found between increased parental escapements and age 1. smolt lengths for the smolt-years 1978–86. Moreover, even though produced from a relatively small escapement of 158 000 in 1983, the resulting 70-mm, 2.6-g age 1. smolts in 1985 were the smallest ever observed, and smaller than those produced (107 and 113 mm) from ~140 000 spawners in both 1977 and 1978. Similarly, the ~89-mm smolts produced in 1986 were from an escapement of ~54 000 sockeye whereas three consecutive and similar sized escapements in 1973–75 produced smolts averaging ~127 mm. That is, the smaller lengths of the first and second brood-year (1985 and 1986) age 1. smolts produced after 3 consecutive yr of extremely large escapements reflected the unusually low forage conditions, which uncoupled smolt sizes from the relationship between previous parent-year (1977–84) escapements and resultant smolt lengths. Thus, without the 1985 and 1986 smolts, we found a significant ($p < 0.01$, *t*-test; $p < 0.005$, Spearman rank correlation) negative correlation ($r^2 = 0.75$) between parental escapements and age 1. smolt lengths during smolt-years 1978–84 (Fig. 7).

Conclusions

Quite clearly, drastic changes have occurred in both the zooplankton community and smolt characteristics concomitant with the development of the Frazer Lake sockeye salmon run. These changes reflect the evolution of Frazer Lake from an obvious recruitment-limited system to a rearing-limited one based on the forage base as categorized by Koenings and Burkett (1987a). Hrbáček (1962), Brooks and Dodson (1965), Galbraith (1967), and others have clearly demonstrated that as a fish stock increases in abundance, size-selective predation will eliminate or reduce to insignificant numbers the larger body size individuals of preferred zooplankter species. Consequently, the highly selective feeding characteristic of sockeye juveniles (Goodlad et al. 1974; Eggers 1978; Koenings and Burkett 1987a) results in the larger, less evasive zooplankter taxa being reduced in

TABLE 5. Comparison of mean temperatures at 1 and 20 m for the two sample stations during both the heating and cooling cycles at Frazer Lake. Also shown is the maximum duration of juvenile sockeye salmon rearing (4°C in the spring to 4°C in the fall) and the separation between heating and cooling cycles by the date of the lake's maximum heat content.

		Heating			Cooling			
Rearing year	Depth (m)	Start date	Mean temperature (°C)	End date	Start date	Mean temperature (°C)	End date	Rearing duration (d)
				Station 1				
1985	1	13 June	8.7	28 August	29 August	8.3	10 November	150
	20	13 June	6.4	28 August	29 August	7.3	10 November	150
1986	1	24 May	6.6	20 July	21 July	8.6	26 September	125
	20	24 May	5.2	20 July	21 July	6.4	26 September	125
				Station 2				
1985	1	13 June	8.7	10 August	11 August	8.7	20 November	160
	20	13 June	7.1	10 August	11 August	8.0	20 November	160
1986	1	24 May	6.4	20 July	21 July	8.3	28 September	127
	20	24 May	5.5	20 July	21 July	7.0	24 September	123

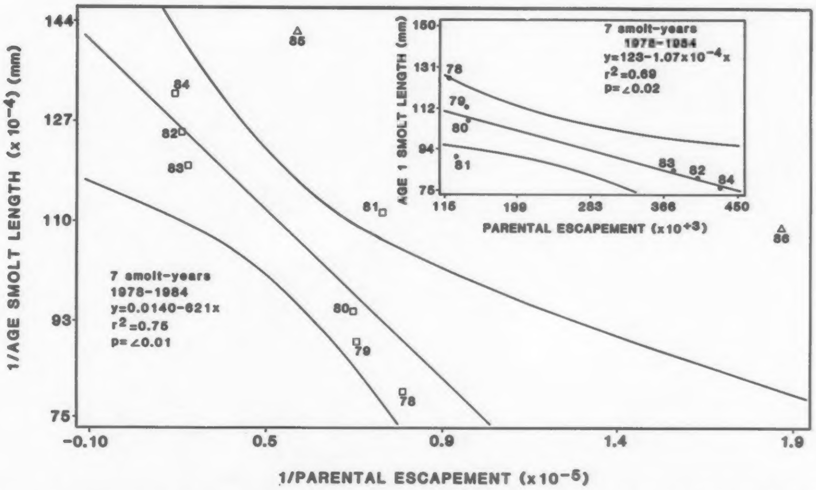

FIG. 7. Regression between transformed parental sockeye salmon escapement and transformed smolt length in Frazer Lake for smolts produced during 1978–84. The regression lines (+95% confidence intervals) have slopes significantly different from zero ($p < 0.001$). Inset shows the nontransformed relationship.

abundance and size before others (Drenner et al. 1978). As zooplankton populations are restructured by increasing predation pressure, feeding of sockeye salmon fry becomes less efficient, fry growth is reduced, and ultimately smolts become smaller until finally reaching a minimal or "threshold" size for smolting (Koenings and Burkett 1987a). In Frazer Lake, as the forage base responded to progressively heavier pressure by predators, the zooplankton community began to resemble predator-resistent communities characteristic of rearing-limited nursery lakes (e.g. Upper Russian Lake) (Fig. 5). Consequently, the juvenile rearing capacity of Frazer Lake has been lowered, as indicated by the meager total zooplankton densities, the minimal size of *Bosmina*, the low density of *Daphnia*, and the decreasing smolt sizes. The increase in lake fertility from nutrients supplied through escapements as high as 486 000 (1985) has served to lessen the decline in total zooplankters, but not the macrozooplankton (Table 4). Excessive planktivory by juvenile sockeye in Frazer Lake may account for the disproportionately small increases in the standing stock of herbivorous macrozooplankters compared with the increase in rotifers, a nonprey item.

It appears the spawning area capacity of ~400 000 forecasted by Blackett (1979) is appropriate at Frazer Lake, as the 1980 brood-year of 405 528 spawners (Table 1) returned a record 749 862 adults, including 589 393 age 2.2 fish (Table 2). However, the large numbers of foraging juveniles from the ~400 000 sockeye escapement overwhelmed the rearing environment. In subsequent brood-years (1981 and 1982), when 377 716 and 430 423 adults entered the lake, respectively (Table 1), a total return of only 40 867 adults was produced from the 1981 brood-year, of which 7748 were age 2.2, and a return of only 3735 age 2.2 adults was produced from the 1982 brood-year (Table 2). Not only was brood-year production lower after the 1980 escapement, but the large number of juveniles rearing in 1981 and 1982 may have reduced the number of age 2. smolts produced from the 1979 escapement. This would help explain the production of only 24 323 age 2.2 adults in 1984 off the 1979 parent-year, i.e. the lack of an increase in production above the low cycle brood-year of 1978 (Table 2). Moreover, the lowered rearing capacity was not countered by short-term decreases in subsequent escapements (1983 and 1984) of 158 340 and 53 524, respectively (Table 1), as resultant smolts were substantially smaller (70 and 89 mm) than those produced from equivalent escapements (Fig. 7) prior to a predator-resistant zooplankton community being formed.

Thus, once the rearing capacity is overtaxed in sockeye lakes, and a predator-resistant zooplankton community forms as in Frazer Lake (Table 3), a lowered efficiency of smolt production will result regardless of smaller spawner density because of lowered productive capacity. Such adverse effects of over-escapements illustrate a basic tenet of determining escapement goals through a spawner–recruit relationship (e.g. Ricker 1958) which mangers could avoid, e.g. the need for spawner densities to overtax either the spawning capacity, rearing capacity, or both in order to reduce adult returns. Since density-dependent, trophic level changes in zooplankton and smolt characteristics relative to increased juvenile rearing densities can be defined, they should either be used in conjunction with or substituted for methods (e.g. spawning and rearing area or spawner–recruitment data) which assume an unchanging rearing environment (Mathisen 1972).

Since fish production is not an exclusive function of spawner density, Rigler (1982) argued that a successful paradigm concerning fish yield must describe the effects of physical and chemical variables as well as other aquatic organisms besides fish. In this more holistic viewpoint, escapement models that do not consider trophic level responses are simply not sufficient to define the capacity of a lake to produce sockeye salmon. Consequently, these models should be used only as a rough estimate of production potential when trophic level data are lacking for stock management. The ability to preserve the integrity of sockeye stocks and concurrently maximize production can only be achieved from matching observed trophic responses to changing escapements as illustrated for Frazer Lake.

Acknowledgements

We thank Bob Burkett, Chief of Technology and Development for the Fisheries Rehabilitation, Enhancement, and Development (FRED) Division of the Alaska Department of Fish and Game, for his advice and support throughout this project. We extend our appreciation to Roger Blackett of FRED Division in Kodiak for kindly providing the data on zooplankton and sockeye salmon smolts and for extensive review of this manuscript. Finally, we acknowledge Richard Yanusz of the Alaska Department of Fish and Game in Soldotna for analyzing the fish stomach contents and the helpful comments of two anonymous reviewers.

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Planktonic Growth of Larval Lobster (*Homarus americanus*) off îles de la Madeleine (Quebec), Gulf of St. Lawrence

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The carapace length of the three planktonic larval and one postlarval stages of *Homarus americanus* was measured for larvae collected off îles de la Madeleine over three summers. Mean larval size did not vary between years or locations around the islands. The size of stages I and II remained constant throughout the summer, but after molting into stages III and IV, larvae diminished in size through the summer. Size frequency distribution became more scattered as larvae grew into more advanced stages. The increase of variance with size between stages I–IV followed the same progression as that observed between stages V–XIII, allowing prediction of the variance associated with mean size at each stage. The size of stage I larvae collected in nine regions along the Atlantic coast was not correlated with the July surface water temperature or with the smallest female size at maturity. Comparison of various body proportions suggested that a single morphometric measurement is not sufficient to describe geographical variations in size. Percentage growth per molt decreased with each successive molt. During summer, increment at molt decreased and molt frequency increased. Larval growth rates followed closely the temperature regime, with maximum growth rate attained during the warmest period of the summer (July 30 – August 9). The duration of the first three larval stages estimated from field data was of 24 d compared with 21 d calculated from previous laboratory studies. The maximum abundance of stage I larvae was synchronized with the period of most rapid increase in summer temperature, thus insuring that larvae achieved highest net growth rates through their planktonic phase.

La longueur du cephalothorax des trois stades larvaires et du premier stade postlarvaire du homard américain (*Homarus americanus*) a été mesurée aux îles de la Madeleine pour trois étés. La taille moyenne des larves de chaque stade ne variait pas selon les régions des îles. Quoique la taille des stades I et II n'ait pas changé au cours de l'été, les larves passant aux stades III et IV étaient de taille progressivement plus petite au cours de la saison estivale. Au fur et à mesure que les larves atteignaient un stade plus avancé, la distribution de fréquence de tailles devenait de plus en plus dispersée autour de la moyenne. L'augmentation de variance avec la taille au cours des stades I–IV suivait la même progression que celle calculée pour les stades V–XIII, permettant de prédire la variance associée à la taille moyenne à chaque stade. Aucune corrélation ne fut observée entre la taille des larves de stade I provenant de neuf régions le long de la côte Atlantique et la température de surface en juillet et la taille à maturité minimale des femelles. La comparaison des rapports entre différents types de mesures indique que la mesure d'une seule caractéristique morphométrique est insuffisante pour discerner les variations géographiques de taille. Le pourcentage d'accroissement à la mue diminuait avec chaque stade de mue successif. Au cours de l'été, on observa une diminution de la croissance à la mue et une augmentation de la fréquence du mue. Le taux de croissance des larves semblait suivre de près le regime thermique, atteignant son maximum durant la période la plus chaude de l'été (30 juillet – 9 août). Les résultats de terrain indiquent que la durée de vie du premier au troisième stade serait de 24 jours, tandis que les travaux en laboratoire rapportent une durée correspondante de 21 jours. L'abondance maximale des larves de stade I est synchronisée avec l'augmentation rapide de température estivale, permettant une croissance rapide pendant la phase planctonique.

Received March 18, 1987
Accepted January 25, 1988
(J9184)

Reçu le 18 mars 1987
Accepté le 25 janvier 1988

The influence of seasonal variations of temperature on the survival of American lobster (*Homarus americanus*) larvae was studied by Caddy (1979), using larvae collected in Northumberland Strait between 1948 and 1963 (Wilder 1953; Scarratt 1964). This study suggested that larvae hatched just before or during the period of peak summer surface temperatures had the best chances of survival, due to the optimal growth rate under such conditions. These results lead us to think that the peak abundance of larvae and maximal growth rates should coincide with the highest rate of increase of summer temperatures. If true, the timing of larval hatching would depend on the rate of increase in temperature rather than on overall seasonal degree-day accumulation. This hypothesis would help explain the absence of linear correlation between the mean surface temperature, larval abundance, and survival in Northumberland Strait (Scarratt 1964; Caddy 1979).

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Geographical variation in thermal regimes is also likely to affect the size and growth rate of larval lobsters over their range (Templeman 1948). In addition to the direct effect of surface temperature on larval size, Templeman and Tibbo (1945) hypothesized that female size at maturity and the average size of spawning females (which are related to bottom temperatures; Aiken and Waddy 1980) could influence the size of egg produced and ultimately that of stage I larvae. Large females captured off îles de la Madeleine were found to carry heavier eggs, containing more energy per gram than those carried by small females (Attard and Hudon 1987). Indirect support was also given by Rogers et al. (1968), who showed that stage I larvae collected offshore, presumably produced by the generally large females found offshore, were larger than larvae collected inshore.

This study documents the size and growth rate of larval lobsters collected in the plankton from various regions off îles de la Madeleine (Gulf of St. Lawrence). Weekly collections took place over the summers of 1978, 1980, and 1981, allowing evaluation of the abundance, production, and horizontal and vertical distribution patterns of the four planktonic stages (Hudon et al. 1986). Size measurements were used to calculate the seasonal variation in growth increment at molt for each stage, thus allowing detailed examination of the relationship between growth rate and abundance and seasonal temperature. We also calculated the expected variability in size around the mean and compared the average mean size off îles de la Madeleine with that found in other geographical areas.

Materials and Methods

Lobster larvae were sampled weekly during the summers of 1978, 1980, and 1981 at a number of stations off îles de la Madeleine. The locations of the sampling stations, gear types, and the duration of sampling periods for each season are described in Hudon et al. (1986). Thirty-eight stations, located around the eastern tip of the islands, in two lagoons, and in Baie de Plaisance (Fig. 1), were sampled from the middle of June to the end of August using either neuston (0–0.15 m) or plankton (0–2.90 m) nets towed horizontally for 30 min.

The larvae collected were sorted according to stage, preserved in 4% formaldehyde, and measured. Cephalothorax length (CL) (from the rear of the eye socket to the back of the carapace, following a line parallel to the medio-dorsal line) was measured to the nearest 0.1 mm under a dissecting microscope. This measurement was selected for its conformity with the method used in the measurement of adults. Other measurements of larval size were made on a subsample of 25 larvae

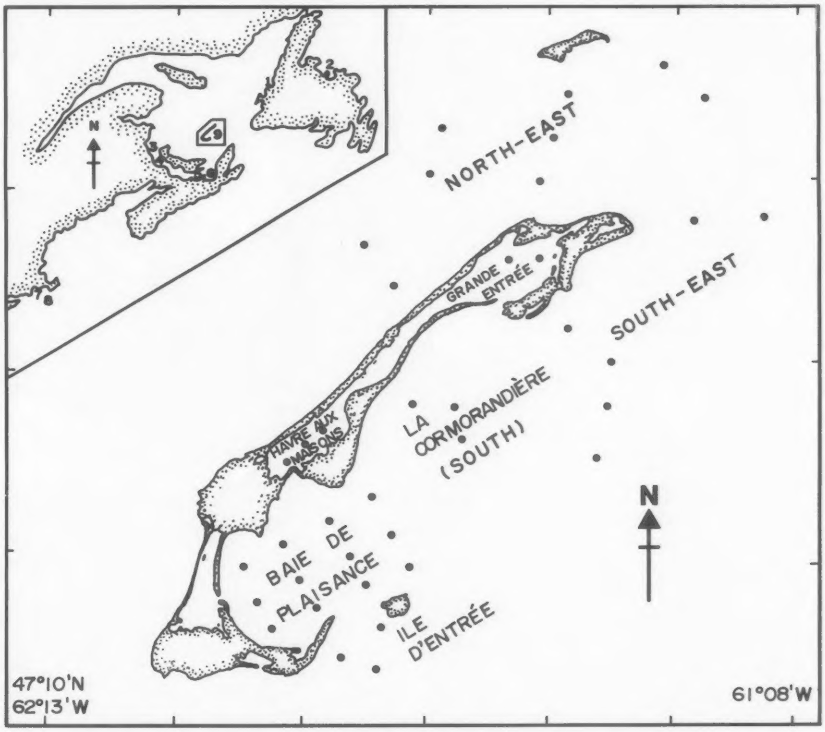


FIG. 1. Location of sampling stations off îles de la Madeleine. The names designate sampling regions and groups of stations. Inset: The Gulf of St. Lawrence with other study areas referred to in the text and in Tables 1 and 2. Location Nos.: 1, Bay of Islands, Nfld.; 2, Notre Dame Bay, Nfld.; 3, western Northumberland Strait; 4, pointe du Chêne, N.B.; 5, Pictou, N.S.; 6, St. Georges Bay, N.S.; 7, inshore southern New England; 8, offshore southern New England; 9, îles de la Madeleine, Que.

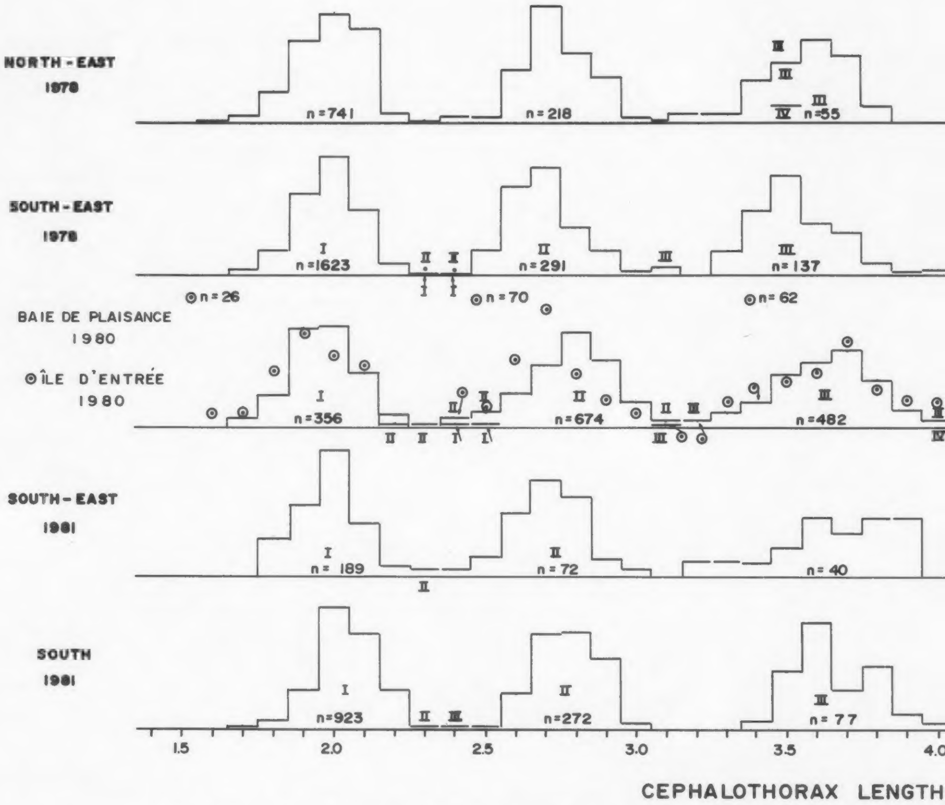
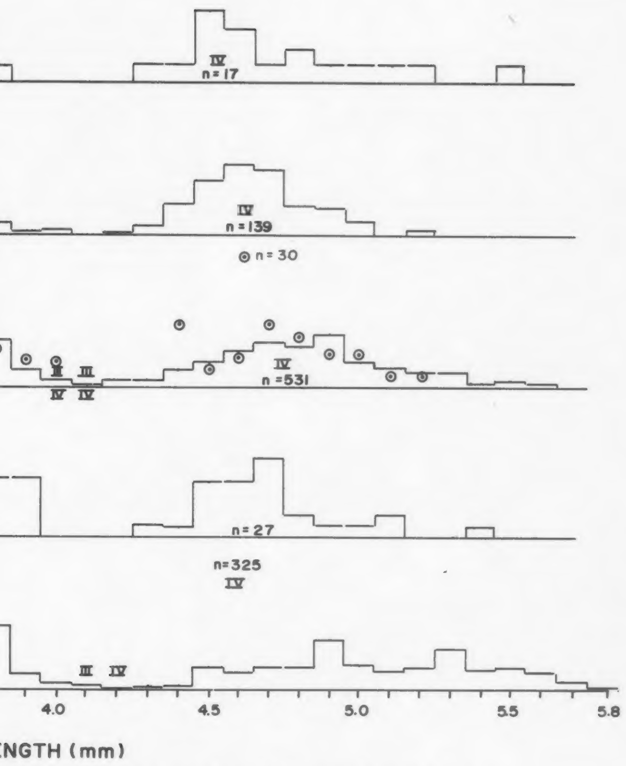


FIG. 2. Size frequency histogram of cephalothorax length for larvae (*n*) captured in different regions seasons. The larval stage is indicated by roman numerals, with arrows to indicate superimposition of larvae captured off île d'Entrée (circles) was superimposed to the histogram of neighbouring ba



t regions off îles de la Madeleine during the three sampling
position of sizes of successive stages. The size distribution
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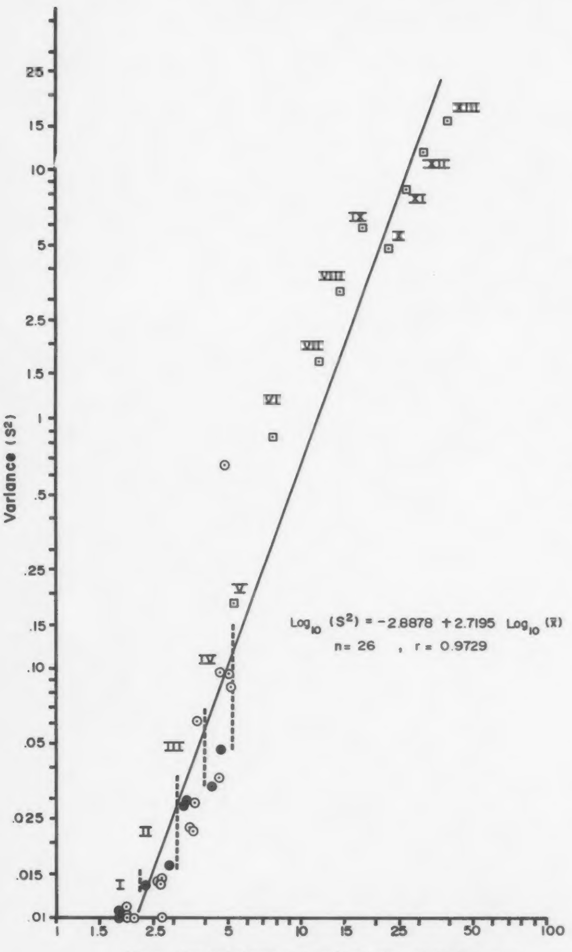

FIG. 3. Linear regression of log-transformed values of the variance on the mean cephalothorax size (log mm). The regression line was calculated using values of mean size and variance for planktonic stages I–IV (circles, this study) and benthic stages V–XIII (squares, Hudon 1987). No significant difference was obtained between the individual regressions of each set of data, thus allowing use of a single relationship to predict the increase of variance with lobster size. Values obtained from Templeman (1948) (solid circles) for stages I–IV, which were not used to calculate the regression equation, closely fit the calculated regression line.

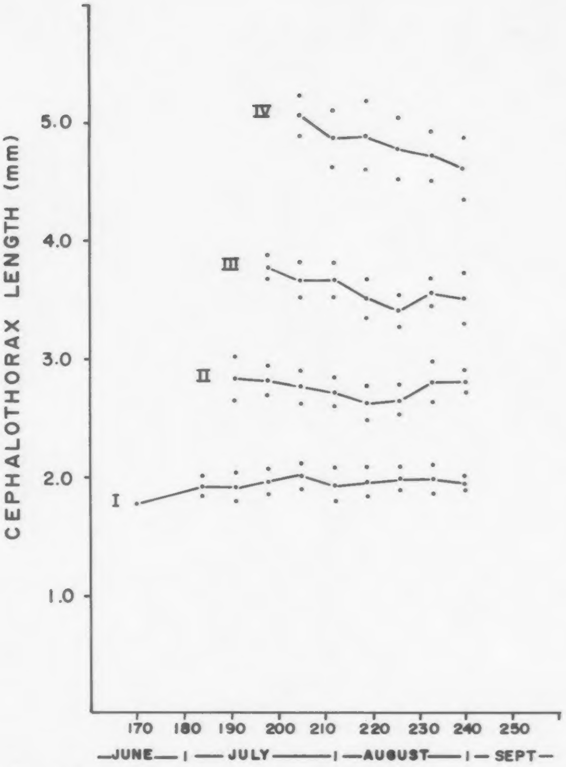

FIG. 4. Temporal variation of mean cephalothorax length for planktonic stage I–IV lobsters captured at the stations in baie de Plaisance. The points on each side of the lines represent 1 SD.

from each stage, from which conversion factors to CL were calculated.

In order to facilitate seasonal and annual comparisons, summer was divided into four periods, corresponding to data on variations in summer temperature. In the course of the first period (June 17 – July 15), surface waters warmed to 14°C. During the second (July 16–29), surface temperature rose from 14 to 16°C, and during the third (July 30 – August 9) from 16 to 18°C. In the fourth period (August 10 – September 2), they fell again to 14°C.

The increase in variability of size was quantified using a power law (Taylor 1961), by the calculation of the regression of the logarithm of variance on the logarithm of mean size. The regression equation of the form

$$(1) \quad \log_{10} S^2 = a + b \log_{10} \bar{x}$$

allowed to prediction of the variance associated with a given size after verifying that the variance followed a similar progression over the entire size range. For this, the regression equation obtained for stages I–IV was compared with that calculated for stages V–XIII (Hudon 1987), with respect to their slope (b) and intercept (a). The homogeneity of slopes was verified and the intercepts compared using analysis of covariance (ANCOVA).

Results

Larval Size

The distribution of sizes of larvae collected in the various regions resembled the Normal distribution for all stages (Fig. 2). Detailed information on the mean sizes and the associated variance registered for each area is presented in Hudon and Fradette (1985). No regional or annual difference was observed, and between areas and years, the modes of the size frequency distributions coincided within 0.1 mm in stages I and II. In stages III and IV, the sizes were more scattered and two modes were observed at île d'Entrée in 1980 and in the southern region in 1981 (Fig. 2). There was very little overlap in the size of successive stages.

TABLE 1. Comparison of various size measurements reported for the four planktonic stages of *Homarus americ* under laboratory conditions. Location No. refers to inset of Fig. 1.

Collection site	Location No.	Carapace length (mm)								Total leng	
		From eye socket[a]				From tip of the rostrum					
		I	II	III	IV	I	II	III	IV	I	II
Laboratory		—	—	—	—	—	—	—	—	7.84	9.20
Laboratory		—	—	—	—	—	—	—	—	8.20	9.60
Fortune Bay, Nfld.		—	—	—	4.54[b]	—	—	—	7.34	—	—
Bay of Islands, Nfld.	1	1.81	2.46	3.25	4.32	3.63	4.56	5.90	7.10	—	—
Notre Dame Bay, Nfld.	2	1.89	2.59	3.45	4.61	3.75	4.78	6.15	7.57	—	—
Port-au-Port Bay, Nfld.		—	—	—	4.29[b] 4.42[b]	—	—	—	6.98 7.18	—	—
West Northumberland Strait	3	1.92	2.58	3.40	4.43	—	—	—	—	—	—
Pointe-du-Chêne, N.B.	4	—	—	—	4.19[b]	3.78	4.84	5.87	6.65	—	—
Pictou, N.S.	5	—	—	—	4.96[b]	3.96	—	—	7.93	—	—
St. Georges Bay, N.S.	6	—	—	—	4.46[b]	3.84	4.99	6.51	7.22	—	—
Southern New England	7	—	—	—	—	3.81	5.09	6.34	7.66	8.32	10.36
Southern New England	8	—	—	—	—	3.95	4.98	6.65	8.00	8.60	10.76
Îles de la Madeleine	9	1.99[b]	2.73[b]	3.60[b]	4.83[b]	—	—	—	—	—	—
North east coast of England		2.74[b]	3.57[b]	4.52[b]	5.60[b]	—	—	—	—	9.82	12.84
Laboratory		—	—	—	—	—	—	—	—	8.00	11.00
Laboratory		2.54[b]	3.13[b]	3.86[b]	4.66[b]	—	—	—	—	—	—

[a] From the bottom of the eye socket to the middle back portion of the carapace, unless otherwise specified.

[b] From the bottom of the eye socket back on a line parallel to the medio-dorsal line.

americanus and *Homarus gammarus* found in nature or grown

otal length (mm)				
II	III	IV	Remarks	Reference
			Homarus americanus	
9.20	11.10	12.60	—	Herrick 1896
9.60	11.40	13.50	—	Hadley 1906
—	—	—	—	Templeman 1948
—	—	14.60	1938	Templeman 1948
—	—		1940	Templeman 1948
—	—	—	—	Templeman 1948
				Templeman 1948
—	—	14.40	—	Wilder 1953
—	—	—	1937	Templeman 1948
—	—	—	1936–1937	Templeman 1948
—	—	—	1938	Templeman 1948
10.36	12.86	15.64	Inshore	Rogers et al. 1968
10.76	13.12	15.87	Offshore	Rogers et al. 1968
—	—	—	Overall mean	This study
12.84	16.58	19.43	*Homarus gammarus*	Nichols and Lawton 1978
11.00	12.00	14.00	—	Williamson 1927
—	—	—	—	Gruffyd et al. 1975

ified.

TABLE 2. Data used to correlate the size of stage I larvae with July mean sea surface temperature and smallest female size at maturity. Values of the Pearson correlation coefficient (r) smaller than the critical probability (p) value $P_{0.05,8} = 0.632$ are not significant (n.s.). Location number refers to inset of Fig. 1.

July mean sea surface temperature (°C)[a]	Smallest female size at maturity (mm CL)[b]	Size of stage I larvae (mm)[c]	Collection site (location No.)
10.6	84.3	3.63	Bay of Islands, Nfld. (1)
9.4	84.3	3.75	Notre Dame Bay, Nfld. (2)
16.4	65.0	3.46[f]	West Northumberland Strait (3)
15.6	64.6	3.78	Pointe-du-Chêne, N.B. (4)
15.0	56.2	3.96	Pictou, N.S. (5)
15.0	56.2	3.84	St. Georges Bay, N.S. (6)
18.9	65.0	3.81	Inshore New England (7)
15.6	80.0[d]	3.95	Offshore New England (8)
13.3	66.0[e]	3.05[f]	Îles de la Madeleine (9)
$r = 0.207$	-0.022		
$p =$ n.s.	n.s.		

[a] U.S. Naval Office 1967.

[b] Data reported from Templeman and Tibbo (1945), unless otherwise specified.

[c] Measured from the tip of the rostrum to the back of the carapace.

[d] Skud and Perkins (1970).

[e] Attard and Fradette (1985).

[f] Length to the tip of the rostrum calculated using a conversion factor from Table 3.

TABLE 3. Comparison of various measurements of larval body size. Mean and variance (parentheses) of 25 larvae of each stage are provided.

Measurement (mm)	I	II	III	IV
Total length	6.95 (0.08)	8.80 (0.11)	10.84 (0.41)	13.97 (0.48)
Carapace length to tip of rostrum	3.30 (0.06)	4.14 (0.02)	5.16 (0.17)	6.62 (0.19)
Eye socket to back of mid-dorsal line (oblique)	1.83 (0.03)	2.52 (0.02)	3.12 (0.10)	4.22 (0.09)
Eye socket to back of carapace (parallel)	2.15 (0.01)	2.73 (0.02)	3.41 (0.07)	4.58 (0.13)

The log-linear increase in variability as related to the increase in size (Taylor 1961) is presented for stages I–IV (this study) and stages V–XIII (Hudon 1987) (Fig. 3). The progression of variance with mean size is described by a single equation, as no significant difference was found between the slopes ($p = 0.1865$) and the intercepts ($p = 0.0580$) using ANCOVA. Additional values for stages I–IV, obtained from Templeman (1948), fall very close to the regression line, although they were not used in its calculation. The equation allows the prediction that a mean size equal to 6.5 mm CL should correspond to a variance of 0.21. If the increase of variance is uniform throughout lobster life (i.e. if the slope of the regression remains the same beyond stage XIII), variance would rise to 169.89 for a cohort of mean size equal to the legal commercial size in Quebec (76.2 mm CL).

Overall mean size for all larvae captured over the three summers equaled 1.99, 2.73, and 3.60 mm CL for larval stages I–III, respectively, and 4.83 mm CL for postlarval stage IV. Whilst the size of stage I and II larvae remained constant, larval stage III and postlarval stage IV sizes decreased throughout the summer (Fig. 4).

Geographical Comparisons of Size

Comparison of average sizes for each stage captured in different locations shows the different types of measurements available (Table 1). For both the American and European lobster, wild larvae were larger than laboratory-reared ones. In the wild, early stages of *H. americanus* are smaller than *H. gammarus*, but the size difference decreases with stage. These measurements allowed us to calculate that the growth increment at molt varied between 20 and 30% per stage for the European lobster and between 30 and 37% for the American species. This observation extends Hadley's (1906) hypothesis that the growth rate of *H. gammarus* is slower than that of *H. americanus* during planktonic life.

The length of the carapace to the tip of the rostrum was the measurement most frequently available and was chosen for geographical comparisons of larval size (Table 2). Comparisons were restricted to stage I, since it was the only stage which in this study remained at a constant size throughout its period of occurrence. Stage I larvae of *H. americanus* ranged from 3.05 to 3.96 mm, the smallest ones being from this study (converted size, Table 3) and the largest taken off Pictou and offshore New

TABLE 4. Percentage of growth increment at molt and mean % increment ($\bar{X}$) between molt stages for each period of the summer. NE, northeast; SE, southeast; BP, baie de Plaisance; LC, la Cormorandiere; IE, île d'Entrée; — = insufficient larval number for calculation.

Period	Area	Year	I–II	$\bar{x}$	II–III	$\bar{x}$	III–IV	$\bar{x}$
1	NE	1978	40.7	40.5	—		—	
(17 June – 15 July)	SE	1978	40.2		—		—	
2	SE	1978	35.5	38.8	31.8	36.7	—	35.3
(16 July – 29 July)	BP	1980	42.3		31.5		38.1	
	LC	1980	38.1		38.2		31.1	
	IE	1980	42.4		34.2		34.8	
	BP	1981	36.2		44.6		33.4	
3	NE	1978	36.9	36.1	32.6	32.8	29.4	35.9
(30 July – 8 August)	SE	1978	35.5		31.8		32.1	
	BP	1980	36.4		35.3		35.8	
	BP	1981	—		—		43.8	
	LC	1981	35.6		31.3		38.4	
4	NE	1978	36.5	35.4	32.7	29.7	33.9	34.2
(9 August – 2 September)	SE	1978	34.5		30.9		33.1	
	BP	1980	42.9		23.7		35.1	
	LC	1980	33.3		29.4		35.3	
	IE	1980	32.0		31.8		34.5	
	LC	1981	33.0		29.9		33.4	

England. No relationship was found between larval size and either the surface temperature in July or the smallest female size at maturity. This latter comparison was made assuming that stage I larvae were captured near their hatching area.

Larval Growth

Mean values for the percent growth increment at molt were calculated for the four summer periods (Table 4). For the three molt groups, the percent growth increment at molt decreased throughout the sampling period. Thus, a stage I larva hatched in the first period of the summer would grow by 40%, while it would gain only 35% in size if hatched in late summer. Similar results were observed for molts II–III and III–IV. Percentage growth increment varied only slightly among periods for the stage III–IV molt. Within a single period, percent growth increment at molt decreased with stage. The difference of growth increment between stages became less important with time. The average duration of each stage can be calculated under natural conditions by using the time at which 50% of cumulative captures was attained (Caddy 1979). In baie de Plaisance, for which a complete record of catches was available in 1981, 7 d would be necessary to go through stage I, 4 d through stage II, and 13 d through stage III (total = 24 d). These values are comparable with the values of 6, 6, and 9 d (total = 21 d) obtained for laboratory-reared larvae at the corresponding temperatures (Templeman 1936). The increasing duration of successive stages is compensated by the accelerated growth rate due to the seasonal warming of surface water.

The curve showing the duration of each stage throughout summer, calculated using Templeman's (1936) equations, was U-shaped for the four stages (Fig. 5), regardless of the area in which they were collected. Stage duration decreased between June 17 and July 29, reaching its shortest duration between July 30 and August 8. Subsequently, the duration of each stage increased again, especially for stage IV postlarvae. Extreme values of duration of each stage observed in all three regions (Fig. 6A) showed differences between baie de Plaisance and the other two regions. In baie de Plaisance the longest durations were observed for stage I and the shortest for stage IV, while the opposite was observed in the northeast and the southeast regions. Postlarvae could spend the total duration of fourth stage in the plankton, or become benthic, thus "disappearing" from the plankton after half of this period (Scarratt 1964). Calculation of the duration of the planktonic stage of postlarvae under both possible scenarios did not alter the seasonal (Fig. 5D) and regional (Fig. 6A) patterns of growth rate. Comparison with regional surface temperatures showed that the duration of larval life decreased as summer temperatures increased until its minimum duration in mid-August, when water temperature reached its peak value at 18°C (Fig. 6B).

A more detailed examination of the duration of the stages in baie de Plaisance (Fig. 7) shows that larvae hatched in mid-June would reach the benthic phase barely 10 d before larvae hatched a month later. The minimal duration of larval development was reached during the first 2 wk of August. The development of larvae hatched after mid-August seemed less predictable, depending on the rate of cooling of surface waters in the autumn.

Data on growth increment at molt and on the duration of each stage allow the calculation of growth (millimetres per day) for the first three stages in the various regions sampled (Table 5). These calculations show that the seasonal decrease in growth increment at molt would be favorably counterbalanced by the shortening of the intermolt period. Growth rate followed very closely the temperature regime, from 0.07 to 0.09 $mm \cdot d^{-1}$ during the first period and 0.13 $mm \cdot d^{-1}$ during the second, to reach a maximum of 0.16–0.22 $mm \cdot d^{-1}$ during the third period. Beyond mid-August, the growth rate decreased again to 0.13–0.14 $mm \cdot d^{-1}$.

Discussion

Our calculation of an average larval size and growth rate over all the samples assumed that food was not limiting and did not

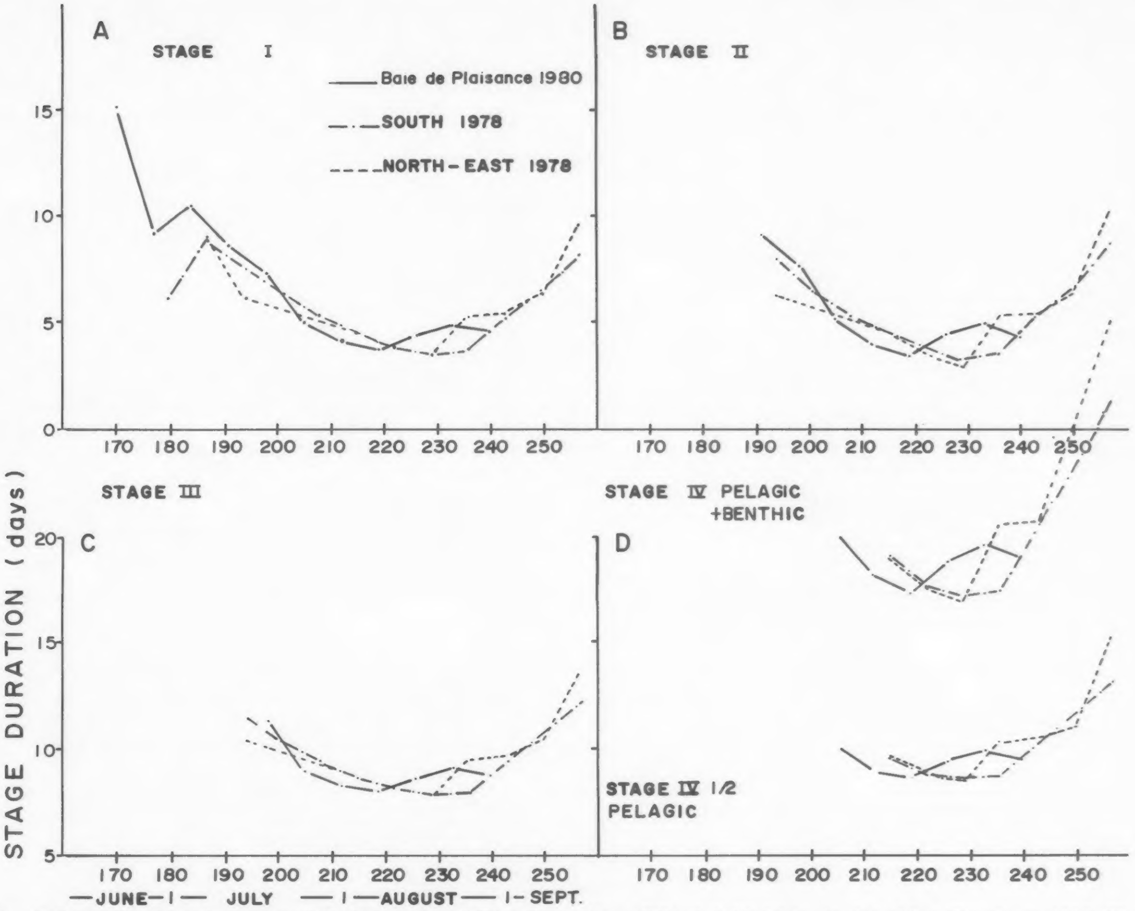

FIG. 5. Seasonal variation in duration of planktonic stages I–IV in three regions off îles de la Madeleine (evaluated from Templeman 1936). The two sets of curves for stage IV illustrate the hypothesis of complete planktonic development (upper curve) and benthic settlement at the middle of stage IV (lower curve).

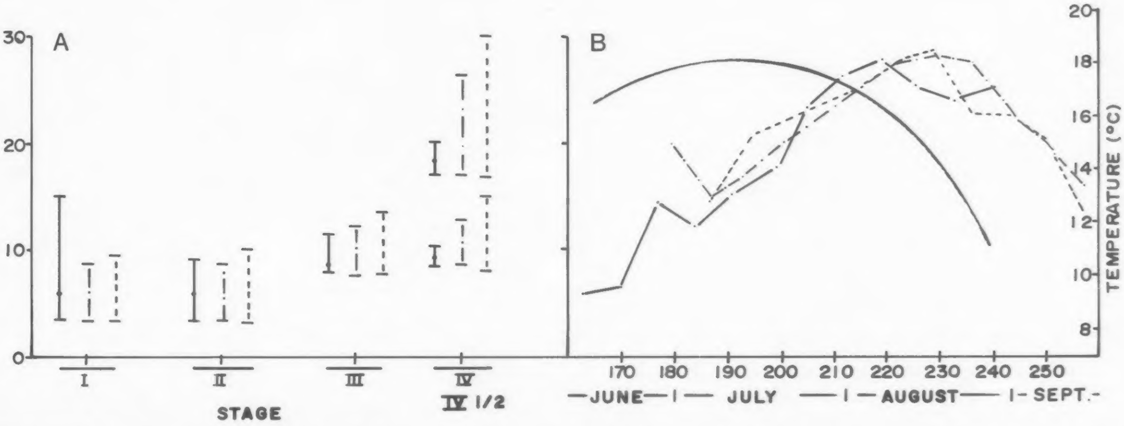

FIG. 6. (A) Extreme values of duration of each stage and (B) Seasonal variation of surface water temperature in three different regions of îles de la Madeleine. The solid line in Fig. 6B indicates water temperature in Northumberland Strait. Symbols are the same as in Fig. 5.

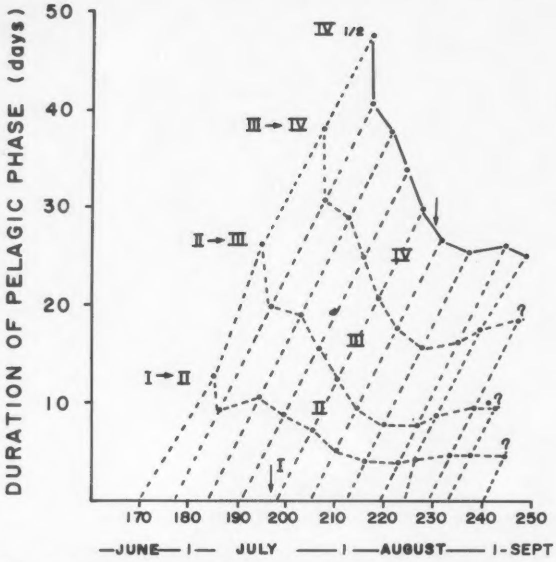

FIG. 7. Duration of the pelagic phase as a function of hatching time in baie de Plaisance in 1980. The vertical arrows indicate the peak of occurrence of stages I and IV, respectively (from Hudon et al. 1986).

exhibit any difference among sampling stations and years of collection. This was supported by the low variability in the percentage growth increment at molt within each period of the summer (Table 4). However, starvation has also been reported to result in an increased duration of the larval stage, without having a direct effect on size (see review by McConaugha 1985). This would lead us to overestimate the growth rate (Table 5), since the duration of each stage under different temperature conditions was obtained from laboratory studies (Templeman 1948). The independent calculation of an average duration using the time at which 50% of the total captures at stage was attained (Caddy 1979) resulted in an estimated duration of 24 d for the first three stages. This value is consistent with the laboratory value of 21 d and would indicate that the growth rates we calculated were realistic for adequately fed larvae in nature.

Comparison among various geographic areas did not show the predicted relationships between the size of stage I larvae with either surface water temperature (Templeman 1948) or female size at maturity (Templeman and Tibbo 1945). However, the absence of such relationships could be at least partly due to the many different sources of larval size measurements, for which variance was seldom considered (see the discussion on sources of error in Templeman 1948 and Wilder 1953). In addition, the choice of variables to characterize the hydrographic conditions and female lobster populations from each area was limited by the lack of uniformity over such a wide geographical area.

It is also possible that a single measurement of size is an inadequate and oversimplified measurement of the adaptive response of lobster larvae to their environment. A comparison of offshore and inshore larvae (Rogers et al. 1968) suggested that multivariate analysis of a number of measurements would be better to distinguish larvae from different areas. The comparison of the ratio of various measurements (Table 3) with similar ratios calculated from the literature (Templeman 1948;

TABLE 5. Calculation of growth rate from values of growth increment and the duration of each stage (from Templeman 1936 and Caddy 1979) from the average temperature in each area during the four periods of the summer. Abbreviations for areas are the same as in Table 4.

			Increment (mm)				Stage duration (d)			Growth rate (mm·d^{-1})		
Period	Area	Year	I–II	II–III	III–IV	T (°C)	I	II	III	I	II	III
1 (17 June – 16 July)	NE	1978	0.81	0.65	—	13	8.8	9.3	12.7	0.08	0.07	—
	SE	1978				13	8.8	9.3	12.7	0.09	—	—
	Avg.									0.09	0.07	
2 (16 July – 20 July)	SE	1978	0.71	0.95	—	15	6.3	6.4	10.4	0.11	0.15	—
	BP	1980	0.83	0.88	1.40	14	7.6	8.0	11.6	0.11	0.08	0.12
	LC	1980	0.75	1.04	1.17	14.5	6.8	6.9	11.0	0.11	0.15	0.11
	IE	1980	0.81	0.93	1.40	15.5	6.1	6.2	10.2	0.13	0.15	0.14
	BP	1981	0.72	1.21	1.31	17.2	4.2	4.3	8.5	0.17	—	0.15
	Avg.									0.13	0.13	0.13
3 (30 July – 8 August)	NE	1978	0.72	0.87	1.04	17	4.5	4.5	8.7	0.16	0.19	0.12
	SE	1978	0.76	0.85	1.13	17	4.5	4.5	8.7	0.17	0.19	0.13
	BP	1980	0.71	0.94	1.29	17	4.5	4.5	8.7	0.16	0.21	0.15
	BP	1981	—	—	1.62	18	3.5	3.2	8.1	—	—	0.20
	LC	1981	0.73	0.87	1.40	18.5	3.2	3.2	7.8	0.21	0.27	0.18
	Avg.									0.18	0.22	0.16
4 (9 August – 2 September)	NE	1978	0.72	0.88	1.21	16.0	5.4	5.4	9.6	0.13	0.16	0.13
	SE	1978	0.68	0.82	1.15	16.5	5.0	5.0	9.2	0.14	0.16	0.13
	BP	1980	0.85	0.67	1.23	16.0	5.4	5.4	9.6	0.16	0.12	0.13
	LC	1980	0.67	0.78	1.21	16.0	5.4	5.4	9.6	0.12	0.14	0.13
	IE	1980	0.64	0.84	1.20	15.4	6.2	6.3	10.3	0.10	0.13	0.12
	LC	1981	0.68	0.82	1.19	17.7	4.0	3.8	8.3	0.17	—	0.14
	Avg.									0.14	0.14	0.13

Wilder 1953; Rogers et al. 1968) indicates that the relative proportions of body parts is highly variable and might be a more adequate indication of change than single measurements. A proportionately short rostrum length for larvae from îles de la Madeleine could explain their substantially smaller converted size (3.05 mm) than observed in other areas (3.46–3.96 mm) (Table 2). A survey using standardized measurements of wild larvae collected together with data on hydrographic conditions and food availability would be necessary to settle this point.

In contrast with stages I and II, a decrease in size was observed over the summer season for stages III and IV. Such a decrease in size with an increase in temperature has been reported for many groups of zooplankters (McLaren 1963; Marshall 1949). This would suggest that metabolic constraints are more important for late stages than for the two first stages. However, a similar effect for stage IV postlarvae could be due to the early disappearance from the plankton of the larger individuals, which could reach the benthic stage more rapidly than smaller ones. A favorable selection would occur for individuals of a large size and/or of a rapid growth rate, thus reducing the duration of planktonic life, during which heavy predation is likely to occur. Larvae hatched in the last period of the summer would experience a very fast growth rate in their early life (Table 5) but, it is hypothesized, may not develop beyond the fourth stage in the event of a rapid cooling of surface water temperature in the fall (Scarratt 1964; Caddy 1979).

A previous study on egg production and development off îles de la Madeleine (Attard and Hudon 1987) showed that eggs produced by large female lobsters hatched earlier and contained more calories per egg than those produced by small females. This observation implies that larvae produced by large females could either be larger or benefit from a larger amount of stored energy in the early posthatch period (Sasaki et al. 1986). In this study, we observed that the size of stage I larvae remained the same throughout the summer (Fig. 4). It is therefore likely that the greater amount of calories in eggs hatching early is used to sustain metabolic needs rather than to increase body size, ensuring a better survival.

Larval abundance data (Hudon et al. 1986) indicated that hatching of stage I larvae peaked during the last fortnight of July. The maximum abundance of stage IV postlarvae occurred in August and coincided with highest summer temperatures (Fig. 6B). The maximum temperature off îles de la Madeleine is reached a month later than in Northumberland Strait (solid line, Fig. 6B). This difference in thermal regime could explain the earlier occurrence of stage I larvae in the southern Gulf of St. Lawrence (Caddy 1979). Off îles de la Madeleine, the peak of hatching of stage I was synchronized with the period of most rapid increase of surface water temperature, so that most of the larvae do enter stage IV by the time surface water temperature reaches its maximum (Fig. 7) (Hudon et al. 1986).

Data on abundance (Hudon et al. 1986) and growth of lobster larvae allow us to estimate that benthic settlement of stage IV individuals should take place in late summer, from mid-August to at least mid-September. This extended period of settlement is likely to result in the co-occurrence of molt stages V–VIII (5.3–14.5 mm mean CL) by the end of the first season of benthic growth (Hudon 1987). Stage IV postlarvae settling to bottom early in the summer may be expected to reach a larger size by the end of their first season of benthic growth, which would possibly enhance their early survival. This element of variability within a cohort is superimposed to the variance in size associated to the mean size of each successive molt stage, which was quantified in this study by a power law (Taylor 1961) (Fig. 3).

In summary, this study measured the size of planktonic lobster larvae and estimated their growth rates in the field. Larvae hatched just before or during the peak period of summer surface temperatures appear to have the best chances of planktonic survival. Newly hatched larvae benefit from the rapid increase in summer temperature, which induces high growth rates. This allows them to spend less time in the plankton and to minimize the duration of their exposure to pelagic predators. Finally, larvae hatched early reach the benthic stage in mid-August, which should allow benthic growth before the fall cooling period. Our results show the crucial importance of scheduling egg hatching with environment conditions allowing quick larval growth through each successive stage in order to optimize survival.

Acknowledgements

The authors thank John Caddy, Ted Grainger, Alex Bielak, and an anonymous reviewer for their comments on earlier versions of the manuscript.

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Laboratory Study of Foraging by Atlantic Mackerel, *Scomber scombrus*, on Natural Zooplankton Assemblages

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Pepin, P., J. A. Koslow, and S. Pearre Jr. 1988. Foraging of Atlantic mackerel, *Scomber scombrus*, on natural zooplankton assemblages. Can. J. Fish. Aquat. Sci. 45: 879–887.

This study reports on the behavioural response of captive Atlantic mackerel, *Scomber scombrus*, to changes in composition and abundance of natural zooplankton assemblages. Filter-feeding activity and swimming speed increase with increasing prey concentration. Swimming speed also increases with increasing prey size. Prey preference shows a size selective pattern that is slightly influenced by the size of the largest available prey, but not by variations in total prey abundance or density of individual size categories. Feeding rates under average natural conditions of prey abundance (0.1 g wet weight·m^{-3}) indicate that mackerel would be unable to satiate during a foraging period restricted to daylight hours. Although prey aggregation or night feeding may enable mackerel to attain their maximum ration in the wild, a review of the literature suggests that pelagic fish seldom satiate. The dynamic response of mackerel to changes in prey abundance can have important consequences to the impact that mackerel and other planktivorous fish may have on the dynamics of multispecies zooplankton and ichthyoplankton communities.

L'étude porte sur la réponse comportementale de maquereaux bleus (*Scomber scombrus*) en captivité à des modifications de la composition et de l'abondance d'assemblages naturels de zooplancton. L'activité de filtrage et la vitesse de nage augmentent avec la concentration des proies. La vitesse de nage augmente aussi avec la taille des proies. Les préférences en matière de proies suivent un régime de sélection en fonction de la taille qui est légèrement influencé par la taille des proies les plus grosses, mais non par les variations de l'abondance totale des proies ni par la densité des catégories de taille. Les taux de consommation dans des conditions naturelles moyennes d'abondance des proies (0,1 g de poids humide · m^{-3}) indiquent que le maquereau ne pourrait pas atteindre la satiété si sa période d'alimentation était limitée à la phase éclairée. Bien que la concentration des proies ou l'alimentation nocturne puissent permettre aux maquereaux d'atteindre leur ration maximale dans le milieu naturel, l'examen de la documentation montre que les poissons pélagiques atteignent rarement la satiété. La réponse dynamique des maquereaux aux changements dans l'abondance des proies peut avoir des conséquences importantes en ce qui concerne les effets que peuvent avoir les maquereaux et les autres poissons planctivores sur la dynamique des communautés plurispécifiques de zooplancton et d'ichtyoplancton.

Received September 3, 1986
Accepted February 9, 1988
(J8926)

Reçu le 3 septembre 1986
Accepté le 9 février 1988

Several species of pelagic schooling fish (e.g. sardine, anchovy, herring, and mackerel) feed primarily on zooplankton (Scott 1920; Savage 1937; Lasker 1970) and are considered important consumers of secondary production (Steele 1974; Andersen and Ursin 1977; Jones 1984). Although species such as herring, anchovy, and mackerel are heavily exploited and are important members of pelagic ecosystems, relatively little is known about their foraging behaviour. Pelagic fish are traditionally treated as block components in production models (Steele 1974; Jones 1984). They are assumed to take a certain proportion of secondary production, regardless of changes in prey abundance or composition. On the other hand, studies of the foraging of freshwater planktivorous fish focus primarily on patterns of prey selection and feeding behaviour, their relationship to optimal foraging strategies, and the consequences to prey populations.

Pelagic fish can maximize their net energy intake by altering their absolute search rate (i.e. swimming speed) as prey abundance and/or composition varies (Ware 1978). Marine planktivorous fish may also alter their pattern of prey selection as prey size composition changes (Koslow 1981). When faced with different prey assemblages, many planktivorous fish can switch their mode of feeding on zooplankton, foraging either by particulate or filter-feeding, in order to maximize their net energy intake (Crowder 1985).

The foraging of marine planktivorous fish has been studied in the laboratory by manipulating simple prey assemblages consisting of large and small prey items (e.g. studies by O'Connell 1972; O'Connell and Zweifel 1972). However, natural situations are seldom so simple. Zooplankton prey assemblages cover a continuum of sizes and the abundance of prey of different sizes is highly variable. We therefore used natural zooplankton assemblages in two laboratory experiments to study the (1) feeding behaviour and (2) prey selection of Atlantic mackerel, *Scomber scombrus*. Results of these experiments will permit us to evaluate (1) whether mackerel feeding behaviour and prey selection for zooplankton serve to maximize energy intake and (2) how the impact of Atlantic mackerel on the zooplankton community may change as prey size composition and abundance vary.

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Atlantic mackerel were chosen for this study because of their potential importance in regulating fishery recruitment (Lett and Kohler 1976; Winters 1976; Cushing 1980) and zooplankton community structure (Koslow 1983). Their resemblance to Pacific mackerel, *Scomber japonicus* and the widespread distribution of the two species (Parrish et al. 1983) make the findings of this study widely applicable.

Materials and Methods

Collection and Holding Conditions for Fish and Plankton

Atlantic mackerel were captured according to Lambert's (1982) specifications. Briefly, adult mackerel from St. Margarets Bay and St. Georges Bay, Nova Scotia, were angled using barbless hooks and quickly, but gently, dropped into a 350-L black fiberglass tank filled with brackish water (20 ppt) containing a sedative level of quinaldine (1 $mg \cdot L^{-1}$). For transportation to the laboratory, the anesthetic level was raised to 2 $mg \cdot L^{-1}$. Upon reaching the laboratory, mackerel were transferred to a 3000-L (2.4 m diameter × 0.7 m depth) holding tank filled with fresh seawater. Fish were allowed to acclimate to laboratory conditions for 3–4 wk. During the first week of acclimation, fish were habituated to our presence by gradually increasing our activity in proximity of the tanks. During the final 2–3 wk, manipulation of objects in the tanks (e.g. pipes, nets, buckets) was gradually increased to minimize disturbing the fish when prey items were introduced.

Experimental facilities consisted of two 3000-L fiberglass tanks joined together by a connecting tunnel. Filtered seawater was supplied at a rate of 5–10 $L \cdot min^{-1}$. To monitor feeding behaviour and swimming speed, tanks were set up indoors where temperature was maintained constant (16°C) and light was provided on a 14 h light : 10 h dark cycle using six fluorescent tubes (Canadian General Electric daylight) placed 1.5 m above the water surface. Feeding selectivity experiments were conducted outdoors under natural light (approximately 14 h light : 10 h dark cycle) and temperature (16–18°C) conditions. Between experimental trials, mackerel were fed to satiation once a day with a variety of frozen fish and shrimp. Mackerel were starved for 24 h prior to each experiment to allow total gut evacuation (Lambert 1985) in order to have a uniform hunger level.

Natural plankton assemblages used in each feeding trial were captured by towing a variety of ring nets (0.5–1.0 m diameter, 80–1050 μm mesh) at very low speed (<0.25 $m \cdot s^{-1}$) on the morning of the experiment. The contents of the codend were immediately diluted into 20-L plastic buckets and placed in a refrigerator (7°C) to prevent overheating and oxygen depletion. Abundance and size composition of prey for each feeding trial were manipulated by combining the catch from different gear types. The combined catch was then split into two equal portions using a Folsom plankton splitter. One half of the sample was used as a control from which the initial taxonomic and size composition of the plankton was determined. The second half was used as prey for the fish. Plankton samples were obtained in Bedford Basin, Nova Scotia, for the experiment on feeding behaviour and swimming speed and in St. Georges Bay, Nova Scotia, for the experiment on feeding selectivity. The zooplankton community of both these areas is similar and characteristic of many coastal regions. The copepods *Pseudocalanus* sp., *Centropages typicus*, and *Calanus finmarchicus* were the most abundant species.

Experiment 1. Feeding Behaviour and Swimming Speed

The experiments on feeding modes and swimming speed were carried out for 5–7 h to evaluate whether behaviour was influenced by prolonged feeding, i.e. changes in hunger level. The plankton concentration in the experimental tank was maintained constant by a steady flow of plankton from a 350-L supply tank located 1.5 m above the experimental tank. A series of perforated air tubes on the bottom of the supply tank kept the plankton well mixed. To maintain a steady flow, a tandem float kept the topmost portion of the airlift siphon 5 cm above the supply tank's water level. A slight current in the experimental tank dispersed the plankton. Preliminary tests showed that plankton concentrations in the experimental tank peaked and remained relatively constant within 30 min of turning on the airlift system. Plankton concentration in the experimental tank was varied by placing different quantities of plankton in the supply tank.

The experimental school consisted of 10 adult mackerel (mean length 35 cm, SD ±2 cm). Swimming speed and behaviour were monitored with a video camera (20-mm lens) placed 2 m above the experimental tank. Basal swimming speed was determined from the fish's behaviour 15 min prior to introducing the plankton. Feeding behaviour (i.e. the incidence of particulate and filter-feeding bouts and swimming speed) was then monitored for 10 min at hourly intervals over the duration of the experiment. Feeding behaviour was classified as particulate feeding if an individual feeding bout lasted less than 0.5 s. Otherwise a feeding bout was classified as filter-feeding. This criterion distinguished particulate feeding, in which the mouth is partially opened and closed rapidly without extension of the opercula, from filter-feeding, in which the mouth is completely opened and the opercula are maximally extended. Swimming speed was estimated by plotting the position of the snout of each fish on a calibrated grid during a frame-by-frame playback of each record. Rough corrections caused by parrallax for variations in depth were made by evaluating whether the fish was swimming in the bottom or surface half of the tank.

Fifteen experimental trials were conducted. Prey concentration in the experimental tank ranged from 0.1 to 1.0 g dry $wt \cdot m^{-3}$. Mean particle size ranged from 80 to 1050 μm. The weighted mean particle size (PS) of plankton offered to the fish was estimated as

$$(1) \quad PS = \frac{\Sigma W_i S_i}{\Sigma W_i}$$

where S_i corresponds to the mean particle size (162, 324, 504, 731, 955, 1050 μm) for a sieve series (80, 243, 405, 602, 860, 1050 μm) and W_i is the sample dry weight obtained from each sieve.

Experiment 2. Feeding Selectivity

A predetermined quantity of zooplankton (0.05–11.0 g dry $wt \cdot m^{-3}$) was introduced into a tank containing an experimental school of 19 adult mackerel (mean length 35 cm, SD ±3 cm, total biomass 6 kg) using a 20-L plastic bucket, half-immersed and tilted at a 45° angle, which was swept around the periphery of the tank approximately 40 cm from the outer wall. This dispersed the plankton throughout the tank. The fish were allowed to feed for 5 min after the onset of the first feeding bouts, which generally occurred within 30 s of introducing the plankton. The duration of the feeding trial and the number of fish were chosen to simulate the effect of an average school of mackerel (mean biomass 8 mt (MacKay 1976), packing density 1.5 kg·m^{-3} (Hewitt et al. 1976), elliptical configuration with axes ratio of 2.1:1 (Squire 1978), swimming speed 1 body length (BL)·s^{-1} in a direction perpendicular to the long axis of the ellipse) passing a single time through a patch of prey. The fish were then herded into the adjacent tank using a small seine net (2.5 × 1 m, 10-mm mesh). The plankton remaining were removed using a seine of similar size fitted with 0.333-mm mesh. The efficiency of this recovery procedure was tested by following the experimental protocol in the absence of mackerel. Recovery rates in the absence of mackerel were independent of the size of plankton and ranged from 90 to 100% (mean 94%) for copepods with prosome lengths greater than 0.6 mm. The recovery rate for copepods with prosome lengths less than 0.6 mm was highly variable and was considered to be unreliable. Consequently, the capture efficiency of Atlantic mackerel for copepods with prosome lengths less than 0.6 mm was not considered in this study.

Analysis of the experimental results consisted of comparing the size–frequency composition of zooplankton remaining at the end of each feeding trial with the half of the original plankton kept as a control. Total zooplankton biomass was determined from displacement volumes and converted to grams dry weight (Wiebe et al. 1975). The size composition was determined by first size-fractionating the plankton with sieves (1050, 602, 243 μm). Each size fraction was then subsampled with a Folsom plankton splitter until 200–500 individuals were available for measurement. Subsamples were placed in 10-cm petri dishes and a silhouette photograph was taken by placing the petri dish onto a piece of 10.2 × 12.7 cm film. The prosome lengths of the copepods were digitized by placing the developed negative in a microfiche reader. Copepod prosome lengths were grouped into nine size categories (0.6–0.75, 0.75–0.90, 0.90–1.05, 1.05–1.20, 1.20–1.60, 1.60–2.00, 2.00–2.40, 2.40–2.80, 2.80–3.6 mm). Size categories containing less than 10 individuals were lumped with the smaller adjacent size category.

Feeding selectivity, or capture success, was measured as the proportion of a size category eaten by mackerel ($1-\{[N_0-N_t]/N_0\}$, where N_0 and N_t are the number of copepods in a given size category at the start and end of an experimental feeding trial). All proportions were normalized using an arcsine square root transformation. We investigated whether the proportion of a size category eaten by Atlantic mackerel was influenced by the number of copepods within that size category (ln (number per cubic metre)), the mean size of that prey category (prosome length (millimetres)), total prey concentration (grams dry weight per cubic metre), and the size of the largest available prey (millimetres) using correlation and regression analysis.

Total prey consumption was estimated as the difference in plankton biomass at the start and end of a feeding trial. Because recovery was not 100%, the results may represent overestimates of the actual consumption rate. Total consumption of plankton was fitted to Ware's (1978) modification of the Holling disc equation (Holling 1959) in which the encounter rate is divided into the foraging speed and the cross-sectional area of the reaction field such that

$$(2)\quad R = \frac{\phi U N}{1 + h\phi U N} T$$

where ϕ is the cross-sectional area of the "effective" reaction field which represents an average for the total zooplankton available (square metres per kilogram of mackerel, U is the foraging speed (metres per second), N is prey density (grams dry weight per cubic metre), h is handling time (seconds per gram dry weight of prey per kilogram of mackerel), T is the total foraging time (seconds), and R is the ingested ration standardized to a unit predator weight (grams dry weight per kilogram of mackerel). The parameters ϕ and h were fitted using maximum likelihood. Swimming speed was estimated from our experimental results, assuming an experimental mean particle size of 700 μm.

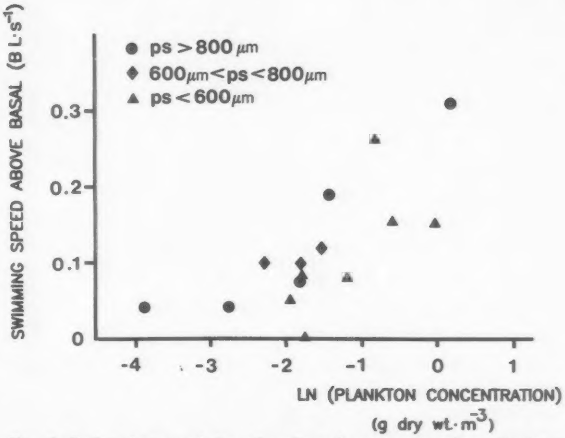

FIG. 1. Swimming speed above basal as a function of total zooplankton concentration and median particle size. Symbols represent experiments with a median particle size (ps) greater than 800 μm (circles), between 600 and 800 μm (diamonds), and less than 600 μm (triangles).

Thirteen experimental feeding trials were conducted. The number of copepod size categories in each feeding trial ranged from three to nine.

Results

In the absence of zooplankton, mackerel swam continuously in a loose school centered approximately 30 cm from the outer wall of the experimental tank. The mouth was slightly agape for respiration. The mean basal swimming speed for mackerel 35 cm fork length, from all experiments combined, was 32 cm·s^{-1} (SD ±2 cm·s^{-1}) or approximately 0.9 BL·s^{-1}.

Atlantic mackerel responded to live zooplankton by increasing their turning rate within 30 s after prey were introduced. Hunter and Dorr (1982) noted a similar pattern for northern anchovy and suggested that it enhances prey encounters when feeding in a patchy environment. The mackerel soon returned to swimming in circuits around the periphery of the tank although the distance between individuals was noticeably less. At the same time, they increased swimming speed and began feeding bouts of varying duration.

In the presence of prey, mackerel swimming speed increased by as much as 0.31 BL·s^{-1} (Fig. 1), or approximately one third of the basal swimming speed. The increase in swimming speed was correlated with both prey concentration and mean prey size

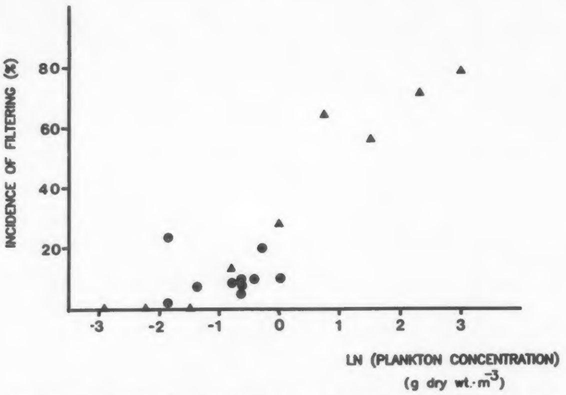

FIG. 2. Incidence of filter feeding (as a percent of total time) as a function of total zooplankton abundance. Circles represent data from this study; triangles represent data from Muir and Newcombe (unpubl. ms., communicated by T. C. Lambert, Bedford Institute of Oceanography, Marine Ecology Laboratory).

(Fig. 1). The equation describing the swimming speed above basal (body lengths per second) as a function of total prey abundance and mean particle size is

$$Y = 0.127 + 0.075 \ln(X_1) + 0.000157X_2 \qquad (r^2 = 0.69, p < 0.01)$$

where X_1 is the total prey concentration (grams dry weight per cubic metre) (t-value = 5.33, $p < 0.01$) and X_2 is the mean particle size (micrometres) (t-value = 2.50, $p < 0.05$). The increase in swimming speed with increasing prey concentration is consistent with Ware's (1978) model predictions based on energy maximization.

The mean percentage of time spent filter-feeding was seldom less than 5% and increased with total plankton concentration (Fig. 2). Our results were combined with those obtained by Muir and Newcombe (unpubl. ms., communicated by T.C. Lambert, Bedford Institute of Oceanography, Marine Ecology Laboratory) to yield the predictive equation

$$Y = 0.242 + 0.136 \ln(X) \qquad (r = 0.75, p < 0.05)$$

where Y is the percentage of time spent filter-feeding and X is the zooplankton concentration (grams dry weight per cubic metre). Data on mean particle size were not available from Muir and Newcombe's (unpubl. ms.) study. However, based on our data, there was no significant influence of mean particle size on the incidence of filter-feeding within the range of prey sizes tested.

Particulate feeding bouts constituted 5–20% of all feeding bouts. The number of particulate feeding bouts did not vary with prey concentration or mean prey size and generally averaged less than 5 bouts·fish^{-1}·min^{-1}. The lack of a significant change in the frequency of particulate or filter-feeding bouts with changes in mean prey size suggests that prey selection may be independent of changes in mean prey size. However, differences in the behavioural response between individuals at the front and rear of a natural school, or at the start and end of our experiments, may allow mackerel to vary prey selection as prey size composition changes.

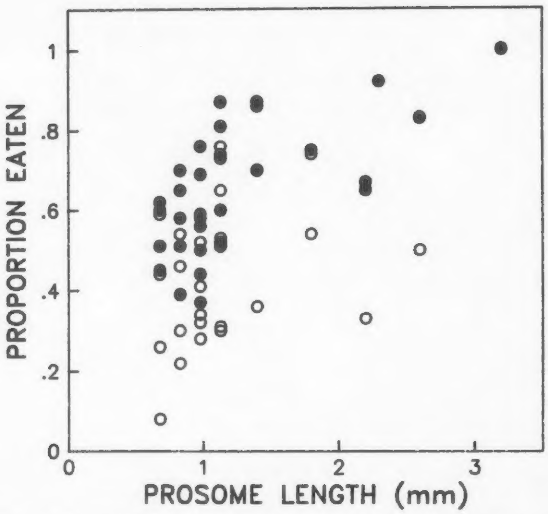

FIG. 3. Proportion of prey eaten by Atlantic mackerel in relation to copepod prosome length. Solid circles represent feeding trials with total prey concentration less than 3 g dry wt·m^{-3}; open circles represent feeding trials with total prey concentrations greater than or equal to 3 g dry wt·m^{-3}.

TABLE 1. Correlation coefficients between experimental conditions and the response by Atlantic mackerel, expressed as the proportion of each size category eaten.

Variable	r	Significance
(1) Prey prosome length (mm)	0.59	$p \leq 0.01$
(2) Total plankton concentration (g dry wt·m^{-3})	−0.39	$p \leq 0.01$
(3) Size of largest prey category in a feeding trial (mm)	0.14	ns
(4) ln (density) for specific size category	−0.23	ns

Predation, expressed as the proportion of each prey size category eaten, by Atlantic mackerel is most strongly influenced by the mean size of each prey category (Fig. 3) ($r = 0.59$, $p < 0.01$) (Table 1). This is consistent with the pattern observed for other marine planktivorous fish (Koslow 1981; Durbin et al. 1981). Other than prey size, total prey concentration is the only variable to significantly influence prey removal ($r = -0.39$, $p < 0.01$) (Fig. 4; Table 1). Regression analysis reveals that total prey abundance and prey size explain 35 and 22%, respectively, of the variance in the proportion of prey categories consumed by Atlantic mackerel. The predictive equation is

$$Y = 0.67 + 0.26X_1 - 0.031X_2 \qquad (r^2 = 0.57, p < 0.01, n = 63)$$

where Y is the arcsin square root transform of the fraction consumed, X_1 is the prosome length of the individual prey size category (millimetres), and X_2 is the total prey abundance (grams dry weight per cubic metre). There is no significant interaction between prey size and total abundance. The decrease in proportion of prey removed with increasing total prey abundance may either reflect a saturation of the predator's functional feeding response, if the decrease in prey removal is equal for

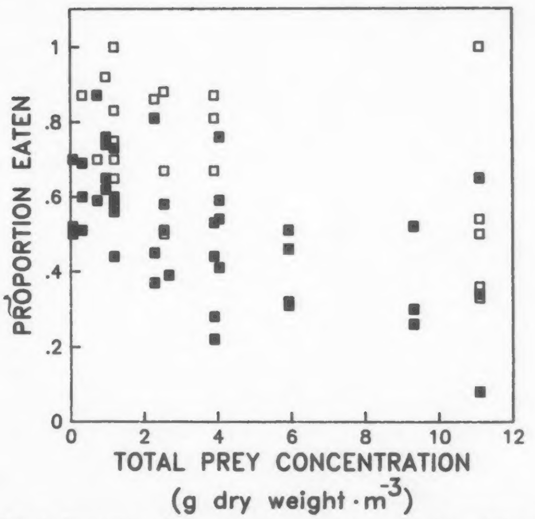

FIG. 4. Proportion of prey eaten by Atlantic mackerel in relation to total prey concentration. Solid squares represent prey less than 1.25 mm prosome length; open squares represent prey greater than 1.25 mm prosome length (maximum 3.4 mm prosome length).

TABLE 2. Correlation between experimental conditions and Manly et al.'s (1972) index of prey preference.

Variable	*r*	Significance
Prey prosome length (mm)	0.46	$p \leq 0.01$
Total plankton concentration (g dry wt·m^{-3})	−0.07	ns
Size of largest prey category in a feeding trial (mm)	0.16	ns
ln (density) for specific size category	−0.10	ns

all prey size categories, or an active shift in prey preference, if the decrease in prey removal with increasing prey abundance is dependent on the size of prey.

Neither density of the individual size categories ($r = -0.23$, $p > 0.20$) nor maximum prey size ($r = 0.14$, $p > 0.20$) had any significant influence on the prey removal by Atlantic mackerel. Either of these variables would be expected to influence predation rates if visual perception of different prey assemblages were to evoke changes in feeding behaviour.

Manly et al.'s (1972) index of prey preference (β) for experiments without prey replacement was used to determine whether there was a shift in preference towards larger prey at high food concentrations or whether the proportion removed decreased similarly for all prey sizes due to a limitation of the predator's functional feeding response. The index of preference was calculated as a modification of Manly et al.'s formula such that

$$(3)\quad \beta = \frac{\log(A_e/A)}{\log(A_e/A) + \log(C/C)}$$

where A_e is the number of plankters within a size category at the end of the experiment, A is the number of plankters within that size category at the start of an experiment, and C_e and C are the number of plankters in all other size categories at the end and the start of an experiment, respectively.

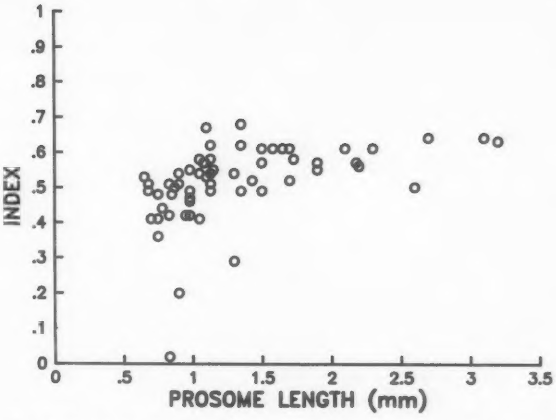

FIG. 5. Manly et al.'s (1972) index of prey preference as a function of prey size (prosome length).

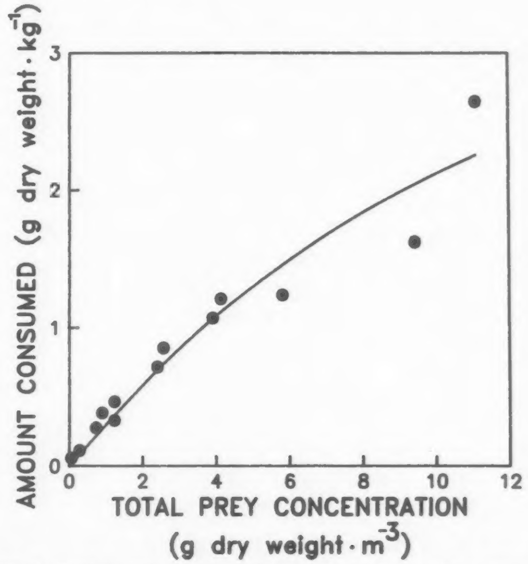

FIG. 6. Total consumption as a function of total zooplankton concentration. Curve represents maximum likelihood fit to the Holling disc equation.

Use of Manly et al.'s (1972) index again indicated that mackerel feeding is size selective ($r = 0.46$, $p < 0.01$) (Table 2; Fig. 5). Copepods greater than 1 mm prosome length tend to be significantly selected by mackerel, while those less than 1 mm are generally a smaller proportion of the ration relative to their numbers in the experimental tank. Total prey abundance had no significant influence on selectivity ($r = -0.07$, $p > 0.05$) (Table 2). There was no shift in prey preference as total prey concentration varied.

Although maximum prey size had no significant effect on the proportion consumed or preference for particular size classes (Tables 1, 2), segregating the data into different size categories (<1, 1–2, >2 mm) shows that the size of the largest available

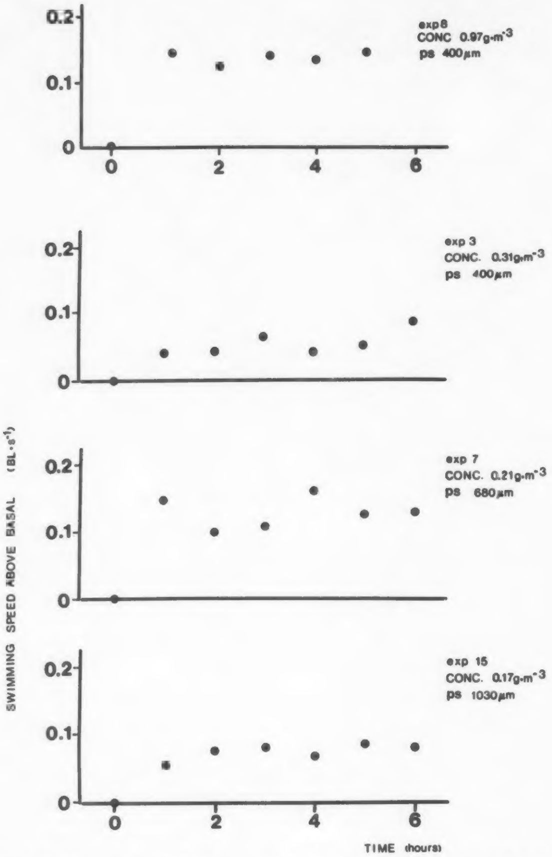

FIG. 7. Examples of the response in swimming speed by Atlantic mackerel as a function of time.

prey has a significant negative effect on the index of preference for copepods of prosome lengths between 1 and 2 mm ($r = -0.46$, df = 27, $p < 0.05$). A similar trend was noted for other size classes, although it was not significant (<1 mm, $r = -0.19$, df = 24, $p > 0.05$; >2 mm, $r = -0.16$, df = 6, $p > 0.05$). Thus, as the size of the largest available prey increases, feeding on smaller prey decreases. This result suggests that there may be some visual recognition, which is associated with particulate feeding, for zooplankton prey by Atlantic mackerel.

Total consumption appears to follow a Holling type II (Holling 1966) functional feeding response (Fig. 6). The cross-sectional area of the effective reaction field for schooling mackerel was 0.00265 $m^2 \cdot (\text{kg mackerel})^{-1}$ and the handling time was 59.4 $s \cdot (\text{g dry wt. prey})^{-1} \cdot (\text{kg mackerel})^{-1}$. The fitted functional feeding response may be biased upwards because of poor recovery of small plankton in our experiments. The residuals from the fitted relationship describing total consumption as a function of total plankton concentration were positively correlated with the size of the largest available prey ($r = 0.61$, df = 11, $p < 0.05$). The larger particle size results in a greater effective search rate, thus increasing the mean rate of food intake.

There was no significant decline in swimming speed during the course of individual experiments (Fig. 7). Thus, over a mean 6-h period, at food concentrations up to 1.0 g dry $wt \cdot m^{-3}$, Atlantic mackerel appeared not to satiate even though their feeding rate might be limited by handling time. From the fitted functional feeding response, we estimate that over the duration of the experiments, individual mackerel may have consumed approximately 9% of their body weight at the highest concentration (1 g dry $wt \cdot m^{-3}$).

Discussion

The results of our experiments indicate that Atlantic mackerel may achieve a higher rate of energy intake by shifting prey preference towards larger prey organisms and by increasing their search rate as prey size and total abundance increase. Both these responses have been suggested as means by which fish may maximize their net energy intake.

Feeding by Atlantic mackerel was size selective (Fig. 3, 5). A similar pattern was observed for a wild mackerel school (school and fish size unknown) whose impact on the zooplankton was observed based on comparative plankton purse-seine hauls to the side and in the wake of the school. The school consumed 31% of *Calanus finmarchicus* (3.0 mm prosome length) and 21% of *Centropages typicus* (1.4 mm prosome length) (P. Pepin, unpubl. data) in their path at a total zooplankton concentration of 0.1 g dry $wt \cdot m^{-3}$. Although this is a lesser grazing rate than the results from our laboratory experiments suggest (90–100 and 70%, respectively), the relative proportion is approximately the same (1.5:1 for field estimates versus 1.4:1 for laboratory results). The slightly higher ratio for the field estimates may partly be due to mackerel not removing all the *Calanus finmarchcus* in the field as they did in the laboratory.

Although there was a decline in the proportion of prey removed with total prey abundance in our experiments, Manly et al.'s (1972) index of prey preference was not significantly correlated with total prey abundance (Table 2). The decrease in proportion of prey eaten as a function of total concentration thus represents a limitation of the functional response by handling time rather than a change in relative selectivity.

Unlike experimental studies with other species of fish (Ivlev 1961; Beukema 1968) which show a shift in prey preference towards larger prey organisms with increasing total prey abundance, mackerel in our experiments show no significant change in relative selection (Table 2) for the size range of organisms included in the analysis. Laboratory studies are often conducted using single fish (Ivlev 1961; Beukema 1968) which are typically offered several prey items at varying densities. Under such conditions, fish may form a search image for a particular prey item. Under natural conditions, marine schooling fish will encounter different prey assemblages. Furthermore, the relative density of different prey organisms will vary from the front to the rear of the school as a result of feeding activity (O'Connell 1972). In contrast with many other planktivores which can only particulate feed, mackerel also have the ability to filter-feed and this may also allow mackerel to make more extensive use of available prey. This does not preclude mackerel from shifting their prey preference in response to other factors.

Mackerel, like northern anchovy (Koslow 1981), showed a significant decrease in prey preference for prey of intermediate size classes (1–2 mm prosome length) ($r = -0.46$, $p < 0.05$) as maximum prey size increased over a 15-fold range in the weight of the largest available prey (1.2–3.2 mm prosome length, 0.148–2.43 mg wet weight; Pearre 1980). This suggests that mackerel feeding consists in part of visual recognition which is characteristic of particulate feeding. Furthermore, a

TABLE 3. Comparison of the net energy gain for two feeding strategies (constant versus increasing velocity) for Atlantic mackerel. Constant velocity is set at 32 cm·s^{-1}. Number in parentheses represents swimming speed (cm·s^{-1}) used in calculation of net energy gain for feeding strategy with increasing swimming speed estimated from our experimental results, assuming a mean particle size of 700 µm. Optimal velocity is the velocity which maximizes the difference between energy intake and the cost of foraging, assuming a mean particle size of 700 µm. See text for further details.

Prey concentration (g dry wt·m^{-3})	Constant velocity: energy gain (kcal·kg^{-1}·h^{-1})	Increasing velocity: energy gain (kcal·kg^{-1}·h^{-1})	Optimal velocity (cm·s^{-1})
0.0	−1.14	−1.14 (32.0)	30
0.2	1.43	1.42 (35.6)	33
0.4	3.96	4.32 (37.3)	43
0.6	6.44	7.32 (38.4)	49
0.8	8.87	10.34 (39.2)	53
1.0	11.25	13.34 (39.8)	56
1.2	13.59	16.32 (40.3)	59

TABLE 4. Estimated time (h) required for mackerel to satisfy rations of 5 and 8% body weight (BW) per day as a function of total prey concentration (g dry wt·m^{-3}) (see text for estimation methods). Swimming speed was estimated from our experimental results assuming a mean particle size of 700 µm.

Zooplankton concentration	5% BW·d^{-1}	8% BW·d^{-1}
0.03	78	125
0.1	22	36
0.2	11	18
0.3	7	11
0.4	5.1	8.2
0.5	4.1	6.5
0.6	3.4	5.4
0.7	2.9	4.6
0.8	5.5	4.0
1.0	2.0	3.2

comparison of predation rates on larval fish from Pepin et al.'s (1987) study, after standardizing prey size into weights, indicates that fish larvae of a given weight are 20–30% less susceptible to predation by Atlantic mackerel than copepods of the same weight. Although behavioural differences between larval fish and copepods may be the cause of the differences in capture efficiency, morphological differences between fish larvae and copepods may affect the apparent prey size perceived by mackerel. These results are in contrast with O'Connell and Zweifel's (1972) conclusions which suggest that mackerel only filter-feed on prey smaller than euphausiids. Mackerel may feed on zooplankton primarily by filter-feeding, and particulate feeding may shift to different prey sizes as the size distribution of available prey changes. This does not imply that the average activity (particulate and filter-feeding) of a school will change as prey size distribution changes. Differences in the size and abundance of prey at the front and back of the school may lead to different behavioural responses within a school. This may result in no net change in behaviour when responses are taken as an average for the school.

In addition to size-selective prey preference, mackerel increase their net energy intake by increasing their swimming speed, as suggested by Ware (1978) and Durbin and Durbin (1983). The higher swimming speeds associated with larger prey sizes (Fig. 1) reflect a greater energy intake because biomass capture efficiency increases with prey size. However, the increase in swimming speed observed for concentrations between 0.1 and 1.0 g dry wt·m^{-3} was only 0.3 BL·s^{-1}, somewhat less than the increase of 1 BL·s^{-1} predicted by Ware (1978) over the same range in prey concentration. This could be due to several factors which affect energy intake; prey retention efficiency, swimming performance, gape size, confinement effects in experimental tanks, differences in reaction field, etc.

Ware (1978) proposed that the increase in swimming speed with increasing prey concentration allowed fish to obtain a greater net energy gain than could be achieved by swimming at a constant speed. To determine if our results (Fig. 2) are consistent with Ware's hypothesis, we compare the net energetic intake estimated from our experiments with the net intake that could be achieved by swimming at a constant speed (basal swimming speed, 0.9 BL·s^{-1}) using the parameters fitted to the Holling disc equation of total consumption, assuming a mean particle size of 700 µm for field conditions, and multiplied by the assimilation efficiency (approximately 95% for mackerel; Lambert 1985). The difference between energy intake and the cost of foraging either at the observed or basal swimming velocities provides a measure of surplus energy. The cost of swimming was calculated from the predictive equations for filter-feeding Atlantic menhaden, *Brevoortia tyrannus*, obtained by Durbin et al. (1981) ($\log_{10}Y = 0.0282X - 1.361$, where Y is the respiration rate (milligrams O_2 per gram per hour) and X is the swimming speed (centimetres per second)). Consumption and respiration rates were converted into kilocalories per kilogram per hour using oxycalorific equivalents of 4.49 kcal·g dry wt. plantkon^{-1}, assuming that carbon is 31% of dry weight (Wiebe et al. 1975) and that calories per gram dry weight = $-227 + 152$(% carbon) (Platt et al. 1969), and 3.29 cal·mg O_2^{-1} (Kleiber 1961). We also computed the optimal swimming speed (maximum net energy gain) given the above parameters for energy intake and cost of swimming.

At a prey concentration of 0.2 g dry wt·m^{-3}, there is no difference in net energy gain (Table 3). As prey concentration increases above this level, it is evident that greater net energy gains may be obtained from increased swimming speed. However, estimates of the optimal swimming speed are much higher than those observed in our experiments (Table 3). If the basal metabolic rate or the rate at which the cost of swimming increases with increasing velocity is greater for Atlantic mackerel than for Atlantic menhaden, then the swimming speeds observed in our experiments may be closer to the optimum level than is suggested from our calculations. Alternatively, mackerel may be capable of increasing their net energy intake in response to changes in prey size and abundance but may not always forage optimally.

The lack of a significant decrease in swimming speed with time (Fig. 6) suggests that mackerel were not satiated even though we estimate they had consumed up to 9% of their body weight in food at the highest concentration (1 g dry wt·m^{-3}). This is higher than previous laboratory results of 5% obtained for various engraulids (Sirotenko and Danilevski 1977; Mikhman and Tomanovich 1977; Hunter and Leong 1981). However, our estimates are within the satiation levels of 8% body weight observed by Ishiwata (1968) for jack mackerel, *Trachurus symmetricus*, and 11% for Pacific mackerel. Field concentrations of zooplankton estimated as the average abundance from large-scale surveys in the Gulf of St. Lawrence and Georges Bank regions average approximately 0.1 g dry wt·m^{-3}

(Bulleid and Stevens 1972; Sherman et al. 1982). At such levels, rations of 2–4.5% body weight per day can be attained by foraging for lengthy periods (14 h, P. Pepin, unpubl. data) depending on the size of available prey. However, average measures of zooplankton abundance may not be suitable to estimate whether mackerel can satiate under natural conditions, since plankton are known to be patchily distributed (Haury et al. 1978).

Table 4 shows the estimated time required to satisfy rations of 5 and 8% of body weight per day at different prey concentrations. In plankton patches with densities greater than 0.2 and 0.3 g dry wt·m^{-3}, mackerel could satisfy rations of 5 and 8% of body weight by foraging in daytime only. If they feed at night, plankton concentrations of approximately 0.1 and 0.2 g dry wt·m^{-3} would be sufficient. However, there is considerable evidence that growth in marine planktivorous fish is food limited (Burd and Cushing 1952; Colebrook 1963; Gulland 1971; Hubold 1978; Hamre 1978; Mathisen et al. 1978; Crawford et al. 1980; Kostrichkina and Oyaveyer 1982). Although mackerel may be capable of achieving high net energy gains in dense plankton patches, the number or extent of these may not be sufficient to allow mackerel to satiate.

Recent food web/chain models (Steele and Frost 1977; Koslow 1983) investigating the consequences of variations in pelagic fish biomass on North Sea plankton dynamics do not incorporate the influence of changes in food availability on the foraging dynamics of the fish. Although shifts in the dominance of large or small plankters associated with low and high levels of fish biomass would still be anticipated from our findings, we suggest that (1) at high levels of secondary production, equilibrium levels of zooplankton will be lower than previously predicted because swimming speed and feeding increase with increased prey availability, (2) this effect should be greatest in systems dominated by larger plankters because of the greater increase in swimming speed observed as prey size and capture efficiency increase, and (3) these differences should decrease at higher predator levels because of the ability of fish to deplete their food resource. Furthermore, we suggest that the response of mackerel of increasing their swimming speed as plankton abundance increases may have important consequences to less abundant members of the plankton community, specifically fish larvae. Although it is believed that high plankton abundance leads to high larval fish survival, high plankton abundance may also be detrimental to larval fish survival if it increases predator search rates but does not lead to satiation of the predator.

The results of this study indicate that the feeding behaviour of Atlantic mackerel (i.e. increased swimming speed with increasing prey abundance and size; preference for larger prey) increases energy intake in comparison with the energetic returns which would be obtained given no behavioural response to changes in prey size or abundance. Whether these patterns are optimal still needs to be determined. However, these conclusions apply to mackerel feeding on zooplankton. Mackerel are known to feed on juvenile fish (Ehrenbaum 1930; Maurer 1976). This may not only alter the response of Atlantic mackerel to changes in zooplankton concentration and size composition but may also alter the degree to which they are food limited. Future research should be directed to the study of foraging when both planktivory and piscivory are possible. Such research could help to understand the influence of mackerel and other marine planktivorous fish on zooplankton community structure as well as on the survival of larval and juvenile fish.

Acknowledgements

The authors would like to thank S. R. Kerr, M. Sinclair, A. J. Bowen, G. Lilly, B. S. Nakashima, D. M. Ware, and an anonymous reviewer for their comments on earlier drafts of this manuscript. T. C. Lambert, J. McRuer, P. Hughes, and T. Verge provided valuable technical assistance. P.P. was supported by postgraduate fellowships from the Natural Sciences and Engineering Research Council of Canada and from the F.C.A.C. fund for the aid and maintenance of research. This research was supported in part through an NSERC strategic grant to J.A.K. and through a Science Subvention grant (Department of Fisheries and Oceans) to S.P. Jr.

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Alternative Harvest Strategies for Pacific Herring (*Clupea harengus pallasi*)

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Hall, D. L., R. Hilborn, M. Stocker, and C. J. Walters. 1988. Alternative harvest strategies for Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 45: 888–897.

A simulated Pacific herring (*Clupea harengus pallasi*) population is used to evaluate alternative management strategies of constant escapement versus constant harvest rate for a roe herring fishery. The biological parameters of the model are derived from data on the Strait of Georgia herring stock. The management strategies are evaluated using three criteria: average catch, catch variance, and risk. The constant escapement strategy provides highest average catches, but at the expense of increased catch variance. The harvest rate strategy is favored for its reduced variance in catch and only a slight decrease in mean catch relative to the fixed escapement strategy. The analysis is extended to include the effects of persistent recruitment patterns. Stock–recruitment analysis suggests that recruitment deviations are autocorrelated. Correlated deviations may cause bias in regression estimates of stock–recruitment parameters (overestimation of stock productivity) and increase in variation of spawning stock biomass. The latter effect favors the constant escapement strategy, which fully uses persistent positive recruitment fluctuations. Mean catch is depressed for the harvest rate strategy, since the spawning biomass is less often located in the productive region of the stock–recruitment relationship. The model is used to evaluate the current management strategy for Strait of Georgia herring. The strategy of maintaining a minimum spawning biomass reserve combines the safety of the constant escapement strategy and the catch variance reducing features of the harvest rate strategy.

On a utilisé une population artificielle de hareng du Pacifique (*Clupea harengus pallasi*) pour évaluer différentes stratégies de gestion, soit une échappée constante par rapport à un taux constant d'exploitation dans le cas de la pêche du hareng rogué. Les paramètres biologiques du modèle ont été dérivés de données sur le stock de hareng du détroit de Géorgie. Les stratégies de gestion sont évaluées en fonction de trois critères : prises moyennes, variance des prises et risques. Une échappée constante fournit les plus hautes prises moyennes mais au dépend d'une augmentation de la variance des prises. On favorise un taux constant d'exploitation à cause de la variance réduite des prises et d'une légère baisse des prises moyennes par rapport à 'échappée fixe. Une analyse plus poussée est effectuée afin d'y inclure l'incidence de régimes de recrutement continu. L'analyse de stock–recrutement porte à croire que les écarts du recrutement sont autocorrélés. De tels écarts autocorrélés peuvent entraîner un biais des estimations de la régression dans le cas des paramètres stock–recrutement (surestimation de la productivité d'un stock) et une augmentation de la variation de la biomasse du stock reproducteur. Cette dernière incidence favorise la stratégie relative à l'échappée constante, qui utilise pleinement les fluctuations positives continues du recrutement. Dans le cas de la stratégie relative au taux constant d'exploitation, les prises moyennes sont diminuées étant donné que la biomasse de reproducteurs est moins souvent située dans le secteur productif de la relation stock–recrutement. On utilise le modèle pour évaluer la stratégie actuelle de gestion du hareng du détroit de Géorgie. La stratégie selon laquelle une réserve minimum de reproducteurs est maintenue allie la sécurité de la stratégie d'échappée constante et les caractéristiques de réduction de la variance des prises de la stratégie du taux d'exploitation constant.

Received March 24, 1987
Accepted February 12, 1988
(J9197)

Reçu le 24 mars 1987
Accepté le 12 février 1988

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Herrring have been exploited off the coast of British Columbia since 1877 (Pearse 1982). A domestic reduction industry developed in the 1930s after the collapse of a pilchard fishery. The 1962–63 season was the peak of the herring reduction fishery, with 240 000 tonnes (t) landed. After 1965 the stocks collapsed, and the reduction fishery was closed indefinitely in 1968 (Hourston 1980).

The fishery for herring sac-roe (ovaries) began after partial stock recovery in the early 1970s. This fishery targets on sexually mature, prespawning herring in late February through April. The objective of maximum prespawning ovary development, combined with too many fishing vessels, creates an intense, often frenzied fishery.

The management strategy for herring fisheries in British Columbia has changed with time. Prior to 1967 the fisheries were managed by catch quota and seasonal closures (Stevenson and Outram 1953). The roe herring fisheries were managed with area-specific constant escapement strategies until 1981 (Hourston and Schweigert 1981). In 1982 a constant harvest rate of 20% of the spawning population became coastwide management policy (Stocker et al. 1983). A modification of the constant harvest rate strategy that provides a minimum escapement level (CUTOFF policy, M. Stocker[2].) is the current management practice. It was suggested that a constant harvest rate strategy would "... provide less variable yields, than fixed escapement policies, and permit informative variation in spawning stock" (Stocker et al. 1983).

The most effective way of testing differences between harvest strategies is through large-scale experimentation (Pearse 1982; Walters 1986). Thus far, deliberate management experimentation is not a policy of the Department of Fisheries and Oceans (DFO). At present, the best available tool for gaining some insights about alternative strategies is simulation modeling. The modeling should serve two purposes: help define the range of experimental choices and provide interim justification for management strategy until experiments are devised and concluded. The objective of this study is to examine alternative management strategies by the technique of computer simulation for Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia, British Columbia.

The analysis is extended to include ideas about cyclic abundance patterns and to evaluate current management practices. Instead of assuming independent, random "environmental effects" every year, the first extension recognizes that there may be persistent periods of good or poor recruitments. This extension represents a significant practical problem that has received only minor attention in the theoretical literature. For a thorough review of theoretical analysis of harvest strategies the reader is referred to Hall (1986). The second extension evaluates the current CUTOFF management strategy for herring in the Strait of Georgia (M. Stocker [2]).

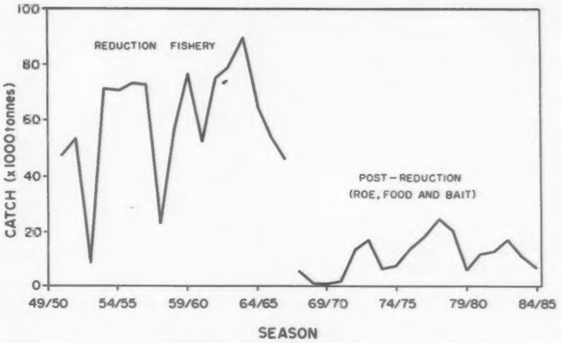

FIG. 1. Commercial herring landings in the Strait of Georgia, 1950–51 to 1984–85 seasons.

TABLE 1. Catch at age used for VPA. Numbers are in millions of fish, 1950–51 to 1984–85 seasons.

	Age										
Year	1	2	3	4	5	6	7	8	9	10	Total
1950–51	0	22	268	149	36	7	2	1	0	0	485
1951–52	68	87	294	138	40	9	3	1	0	0	640
1952–53	0	10	57	29	4	1	0	0	0	0	103
1953–54	0	21	367	250	80	23	6	1	0	0	750
1954–55	0	32	348	282	49	11	3	1	0	0	726
1955–56	0	47	239	217	173	39	6	2	0	0	724
1956–57	0	39	411	155	81	47	5	1	0	0	740
1957–58	0	27	143	56	15	13	7	1	0	0	262
1958–59	5	110	435	121	23	5	5	2	0	0	706
1959–60	0	103	364	285	48	16	4	2	0	0	823
1960–61	0	149	159	137	88	30	5	1	0	0	569
1961–62	1	121	485	142	46	29	9	3	0	0	834
1962–63	0	169	458	248	41	11	5	1	0	0	932
1963–64	0	48	517	280	41	10	4	1	0	0	902
1964–65	27	120	310	173	27	9	3	1	0	0	670
1965–66	0	110	168	118	86	15	6	1	0	0	503
1966–67	50	157	270	83	19	7	1	0	0	0	588
1967–68	20	17	24	10	3	1	1	1	0	0	77
1968–69	3	7	3	1	0	0	0	0	0	0	15
1969–70	0	3	7	1	0	0	0	0	0	0	11
1970–71	1	4	6	6	1	1	0	0	0	0	18
1971–72	0	10	41	39	22	4	1	0	0	0	119
1972–73	0	2	41	30	28	21	5	1	0	0	130
1973–74	0	1	6	13	13	10	3	1	0	0	47
1974–75	0	2	12	21	16	6	2	0	0	0	59
1975–76	0	4	11	38	31	13	5	1	0	0	103
1976–77	0	3	53	35	40	13	4	1	0	0	150
1977–78	0	3	57	75	33	30	10	1	1	0	210
1978–79	0	2	19	51	56	15	7	2	0	0	153
1979–80	0	1	12	8	14	9	2	1	0	0	47
1980–81	0	3	23	28	17	18	7	1	0	0	97
1981–82	0	3	25	23	23	9	11	6	1	0	101
1982–83	0	2	24	37	30	22	8	7	2	0	133
1983–84	0	6	20	25	19	11	5	1	0	0	89
1984–85	0	12	17	13	10	7	3	1	0	0	63

Methods

To evaluate the effects of alternative harvest strategies on the Strait of Georgia herring population, it is necessary to begin with a model that encompasses some essential dynamic processes: growth, reproduction, and mortality. The approach is (1) conduct a virtual population analysis (VPA) for the Strait of Georgia herring, (2) develop a relationship between parent stock and juvenile production based on the results of the VPA, and (3) define the age-structured model mathematics, based on the results of the VPA and subsequent analysis.

Data Sources

Although catch records date back to 1888, reliable records of the place, date, and quantity caught are available only since

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[2] M. Stocker. Estimates of equilibrium biomass in the absence of fishing and corresponding CUTOFF levels for B.C. herring. Unpublished report presented to the Herring Stock Assessment Committee, September 1985.

1950. Catch landings have been sampled since 1933. Spawn surveys indexing escapement began in 1937. We limited our analysis to the period 1950–85. During this period the Strait of Georgia herring population has fluctuated considerably and has been subjected to a wide range of fishing pressure.

The main data inputs for this study are commercial catch, age composition, and average weight at age from catch samples. These data are available in computer files in a consistent format for the period 1950–85 (V. Haist, pers. comm.). Three fisheries have operated during this period. The data for the 1950–51 to 1966–67 seasons are from the reduction fishery. Data for 1967–71 are from a small food and bait fishery. Data since 1972 are from seine and gillnet catches in the roe fishery and the persistent food and bait fishery. Although seine and gillnet catch data are from two gear types within one fishery, it will simplify later descriptions if we refer to the data from seine and gillnet as if from separate fisheries. Figure 1 presents catch for 1950–51 to 1984–85 seasons.

Virtual Population Analysis

Virtual population analysis is a tool that can be used to rebuild a stock history based on information that is often collected in a managed fishery (Gulland 1983). There are two basic information requirements for VPA: catch at age and an estimate of natural mortality. For the analysis to include estimates of younger age classes in recent years, an estimate of fishing mortality in the most recent year is needed.

The table of catch at age in numbers used by VPA (Table 1) is estimated from the general equation

$$(1)\quad C_{a,t} = \sum_{i=1}^{3} (\text{total catch by gear}_{i,t})p_{i,a,t}$$

where p is the catch proportion determined by catch sampling, i refers to the gear type, and a is the age group. In the years of one fishery (1951–71), the equation reduces to $C_{a,t} = C_{tp_{a,t}}$. The summation is needed for 1972–85, when catch at age is summed for the three operating fisheries. We have adopted the aging conventions outlined in Stocker et al. (1985). For example, spawn for the 1950–51 season is deposited in March and produces the 1951 cohort of the 1951–52 season (age 1 fish).

The other requirement for VPA is an estimate of natural mortality (m). Any estimate of natural mortality is uncertain because of the problems of the estimation procedures confounding m with mortality due to fishing, the catchability coefficient q, and the proportion of fish at age maturing. The standard estimate of m for Strait of Georgia herring is 0.45 (Ware 1985). Walters et al. (1982) suggested that standard methods for estimating natural mortality will underestimate m if the proportion of fish at age maturing is not included. The estimates that Walters et al. (1982) arrived at are somewhat higher than the standard DFO estimates. For analytical stock assessment procedures that allow m to vary in relation to biomass, the estimates range from 0.30 to 0.73 (Stocker et al. 1983). We use the age-specific annual survival rates from Walters et al. (1982) (Table 2).

Virtual population analysis works backward from the oldest age class in the most recent year (age 10, 1985). To estimate incomplete cohorts that are currently being fished and new cohorts that are entering the population, estimates of the current exploitation rate, or catchability at age (q_a) and annual effort (E_t), are required. We estimate the numbers of fish in age classes 1–9 in 1985 by $N_a = C_a/E\bar{q}_a$, where N_a = number of fish at age, C_a = catch at age, E = effort, and $\bar{q}_a$ = average catchability at age. Catchability at age is calculated as

$$(2)\quad q_a = \frac{C_{a,t}m_a}{E_t(N_{a,t} - N_{a+1,t+1} - C_{a,t})} .$$

Average catchability at age ($\bar{q}_a$) is calculated as the mean q_a since the start of roe fishing in 1972. Estimates of effort are notoriously poor for clupeid purse-seine fisheries (MacCall 1976). The shift from the reduction fishery to the roe fishery, increasing gear efficiency, and multiple gear types confound any standard estimate of effort. Instead we use an index of effort (Walters et al. 1982), $E = -\ln(1 - \text{harvest rate index})$, where the harvest rate index is estimated each year as catch divided by catch plus the spawning population estimated from spawn surveys by methods detailed in Hourston and Schweigert (1981). This procedure amounts to using the spawn survey population estimates as the terminal numbers except for an adjustment obtained by averaging age-specific catchability over time.

With the 1985 number at age estimates in place, the cohort analysis proceeds from 1985 working backward to 1951 by

$$(3)\quad N_{a,t} = N_{a+1,t+1}/S_a + C_{a,t}$$

where S_a is age-specific annual survival. Equation (3) is from Ricker (1975, p. 198), with $1/S = e^{m}$. This approximation of the standard VPA equation is possible when natural mortality can be ignored during the short fishing season (Type 1 population, Ricker 1975, p. 10). The abundance of age 11 fish is assumed to equal 0, so the number of age 10 fish is catch plus spawners, estimated by the age 10 catch divided by the harvest rate in year t.

Stock and Recruitment

The results of the VPA are number of fish at age before harvest (Table 3). These results are used to define a relationship between parent stock and juvenile production in the theory of stock and recruitment (Ricker 1954). We assume that density-dependent and environmental effects can be represented by the stochastic Ricker model:

$$(4)\quad N_{1,t+1} = \text{Eggs}_t\, e^{\alpha - \beta \text{Eggs}_t + v_t}$$

where N_1 = number of age 1 recruits, Eggs_t = number of eggs spawned, α = maximum recruitment per Eggs_t, β = unhar-

TABLE 2. Age-specific parameters used in the model.

Parameter	Age 1	2	3	4	5	6	7	8	9	10
Annual survival	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.37	0.3	0.25
Proportion mature	0.0	0.1	0.4	0.7	0.9	1.0	1.0	1.0	1.0	1.0
Fecundity (1000 eggs/female)	0	13	17	25	30	30	29	31	32	33
Weight (g)	13	58	83	109	128	144	159	169	171	192

TABLE 3. Millions of fish at age for 1950–51 to 1984–85 seasons from VPA for the Strait of Georgia herring.

	Age										
Year	1	2	3	4	5	6	7	8	9	10	Total
1950–51	5868	2005	865	344	87	14	4	1	0	0	9 187
1951–52	8945	2934	991	298	97	26	4	1	0	0	13 296
1952–53	5745	4438	1424	349	80	29	8	0	0	0	12 073
1953–54	3020	2872	2214	683	160	38	14	4	0	0	9 004
1954–55	3758	1510	1426	923	216	40	7	4	1	0	7 885
1955–56	4189	1879	739	539	321	84	14	2	1	0	7 768
1956–57	6911	2095	916	250	161	74	22	4	0	0	10 433
1957–58	4296	3456	1028	252	47	40	13	8	1	0	9 142
1958–59	3230	2148	1714	443	98	16	14	3	3	0	7 668
1959–60	5574	1613	1019	640	161	38	5	4	0	1	9 055
1960–61	5375	2787	755	327	177	57	11	1	1	0	9 491
1961–62	5431	2688	1319	298	95	45	13	3	0	0	9 891
1962–63	2628	2715	1284	417	78	25	8	2	0	0	7 157
1963–64	1643	1314	1273	413	85	19	7	1	1	0	4 755
1964–65	1540	821	633	378	67	22	4	1	0	0	3 467
1965–66	648	757	351	161	102	20	6	1	0	0	2 046
1966–67	834	324	324	92	22	8	2	0	0	0	1 606
1967–68	1979	392	83	27	4	1	1	1	0	0	2 488
1968–69	2347	980	188	30	8	0	0	0	0	0	3 553
1969–70	2434	1172	486	92	15	4	0	0	0	0	4 203
1970–71	1787	1217	585	240	46	7	2	0	0	0	3 883
1971–72	2291	893	607	289	117	22	3	1	0	0	4 224
1972–73	3961	1146	441	283	125	47	9	1	0	0	6 013
1973–74	3495	1980	572	200	126	48	13	2	0	0	6 436
1974–75	5714	1747	990	283	93	57	19	5	0	0	8 908
1975–76	3803	2857	873	489	131	39	25	9	2	0	8 226
1976–77	1470	1901	1427	431	226	50	13	10	3	0	5 530
1977–78	1839	735	949	687	198	93	18	4	3	1	4 527
1978–79	1352	920	366	446	306	83	31	4	1	1	3 509
1979–80	1101	676	459	173	198	125	34	12	1	0	2 778
1980–81	729	550	338	224	83	92	58	15	4	0	2 092
1981–82	655	364	274	157	98	33	37	25	5	1	1 650
1982–83	1194	328	180	125	67	38	12	13	7	1	1 964
1983–84	5814	597	163	78	44	18	8	2	2	1	6 727
1984–85		2907	296	71	27	12	3	1	0	1	3 318

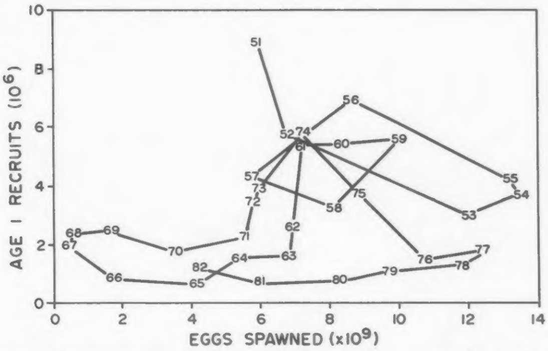

FIG. 2. Stock and recruitment data for Strait of Georgia herring, 1951–82 (number of age 1 recruits versus number of eggs spawned). Years of observations are connected to show time trends. Note poor recruitments since 1976.

vested equilibrium stock size, and v_t = error term (mean = 0, variance = σ_v^2.

The parameters α, β, and σ_v^2 are estimated from the linear regression

$$(5)\quad \ln(N_{1,t+1}/\text{Eggs}_t) = \alpha - \beta\,\text{Eggs}_t + v_t$$

where α is the intercept, β is the slope, and σ_v^2 the variance of the residuals (v_t).

The estimate of the number of eggs spawned in year t is calculated differently for the reduction and roe fisheries. For 1951–71:

$$(6)\quad \text{Eggs}_t = \sum_{a=1}^{10} (N_{a,t} - C_{a,t})\,P_{a,t}\,F_a\,0.5$$

and for 1972–85:

$$(7)\quad \text{Eggs}_t = \sum_{a=1}^{10} (N_{a,t}P_{a,t} - C_{a,t})\,F_a\,0.5$$

where N is number, C is catch, P is the proportion mature, F is fecundity, and 0.5 is the proportion female. The difference between equations (6) and (7) is the position of the catch term. Equation (6) describes the reduction fishery removing fish from the entire population (mature and immature). In equation (7), catch is removed from only the mature population that has migrated onshore to spawn.

Age-specific fecundities and maturities are listed in Table 2. Fecundity estimates are from Hourston et al. (1981). The maturity schedule is from Walters et al. (1982) derived from coastwide age compositions; it is similar to recent data presented by Hay (1985) for ages 5+. We assume less proportion mature for age 4 and younger compared with more recent data presented by Haist and Schweigert (1986). The proportion female is assumed to be 0.5 for all ages. The stock and recruitment data are presented in Fig. 2 and Table 4. We eliminate the last three years (1983–85) of VPA data used for stock–recruitment analysis to reduce the dependence of recruitment estimates based on uncertain information from incomplete cohorts.

The residuals from the regression equation (5) are plotted in Fig. 3. The assumption of random, normal deviates (v_t) from the stock–recruitment equation (4) appears to be violated. A "periodic" nature to the recruitment process is evident. Walters (1985) outlined two sources of bias that confound standard regression techniques normally used to estimate the Ricker parameters (α and β) of equation (4): (1) large measurement errors in the independent variables, such as spawning biomass estimates, and (2) correlations between deviations and subsequent levels of the independent variables. It is likely that both biases affect the herring stock–recruitment data. To measure the effect on parameter estimates of α and β, we did Monte Carlo simulations of the deviation feedback bias in the presence of autocorrelated deviations, using known α and β parameters and an autoregressive function discussed below. Figures 4a and 4b show the dual effect of the biases on α and β. The Ricker parameter α is overestimated by about 10% and the parameter β is overestimated by about 18%. Correcting for these biases will make the stock appear less productive (lower α) and to have a higher unfished equilibrium biomass (higher α/β). The results of the simulation were used to correct the standard regression estimates of α and β as follows: α is decreased by 10% to 2.35 and β is decreased by 18% to 0.00133.

Simulation Model

Tester (1948) first speculated that catch trends apparent in Fig. 1 might reflect some cyclic phenomenon. The factors that might cause such a periodic fluctuation have received much attention (Stocker et al. 1985; Ware and McFarlane 1986; Walters et al. 1986). The model need not be concerned with the

TABLE 4. Stock–recruitment data from VPA, 1951–82 (α = 2.61, β = 0.00162, σ_v^2 = 0.79).

Year	Eggs spawned (× 10⁹)	Age 1 recruits (× 10⁶)	Year	Eggs spawned (× 10⁹)	Age 1 recruits (× 10⁶)
1951	590	8945	1967	44	1979
1952	672	5745	1968	61	2347
1953	1198	3020	1969	164	2434
1954	1349	3758	1970	347	1787
1955	1318	4189	1971	559	2291
1956	858	6911	1972	588	3961
1957	571	4296	1973	574	3495
1958	809	3230	1974	707	5714
1959	996	5574	1975	880	3803
1960	831	5375	1976	1074	1470
1961	717	5431	1977	1238	1839
1962	690	2628	1978	1175	1352
1963	678	1643	1979	974	1101
1964	539	1540	1980	824	729
1965	414	648	1981	597	655
1966	175	834	1982	417	1194

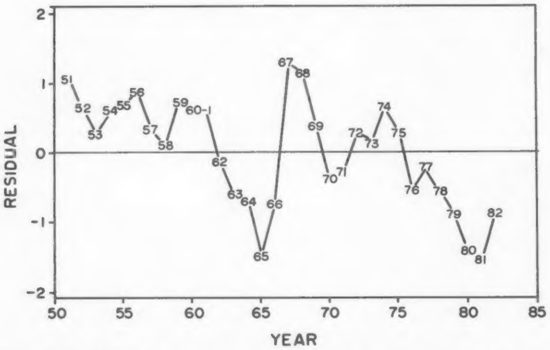

FIG. 3. Residuals from regression of ln(recruits/eggs spawned) against eggs spawned plotted over time. Note cyclic tendency of residuals, representing persistent periods of good or poor recruitment.

cause of population fluctuations, provided that it can mimic those fluctuations in a statistically realistic manner. Likewise, the choice of the stock-recruitment model is not particularly significant. The suggestion from Fig. 2 is that the best recruitments are from intermediate stock sizes, so we use the Ricker model. The recruitment variability expressed in the residual variance of the regression (equation (5)) is so high that any model fits poorly. Our use of a stock–recruitment function is best described by Walters (1986):

> It has been suggested that recruitment should be modeled as a fundamentally stochastic and unpredictable process, with the stock–recruitment function viewed as a collection of probability distributions (one for each level of spawning stock). In this view, the stock–recruitment curve is a description of how average recruitment varies with reproducing stock (and is therefore useful for analysis of long-term average responses to various harvesting policies), without pretense that the curve is at all useful for short-term predictions.

The equations that follow may obscure what is essentially a simple model. We will first describe the action of the model in words.

(1) The model always begins with the same size population.

(2) Catch is removed from the adult population.

(3) The remaining adult population reproduces.

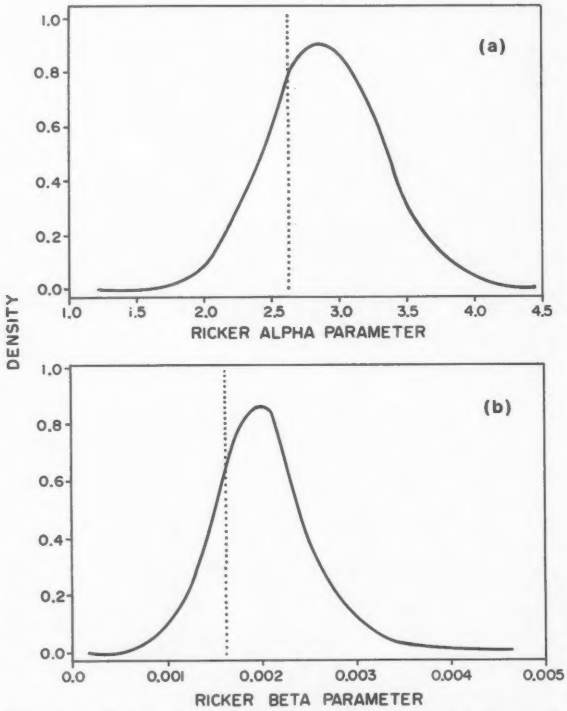

FIG. 4. (a) Effect of bias in correlations between deviations and between deviations and subsequent levels of recruitment on the Ricker stock–recruitment α parameter. The dotted line shows the true α given the model. The probability density function (Chambers et al. 1983) describes the frequency of occurrence (1000 trials). Correlated deviations bias estimates of α by about +10%. (b) Ricker stock–recruitment β parameter for the same simulation as in Fig. 4a. Correlated deviations bias estimates of β by about +18%.

(4) Next year's age 1 fish are determined from reproduction.

(5) Next year's age 2–10 fish equal this years age 1–9 times survival rates.

(6) The model returns to step 2.

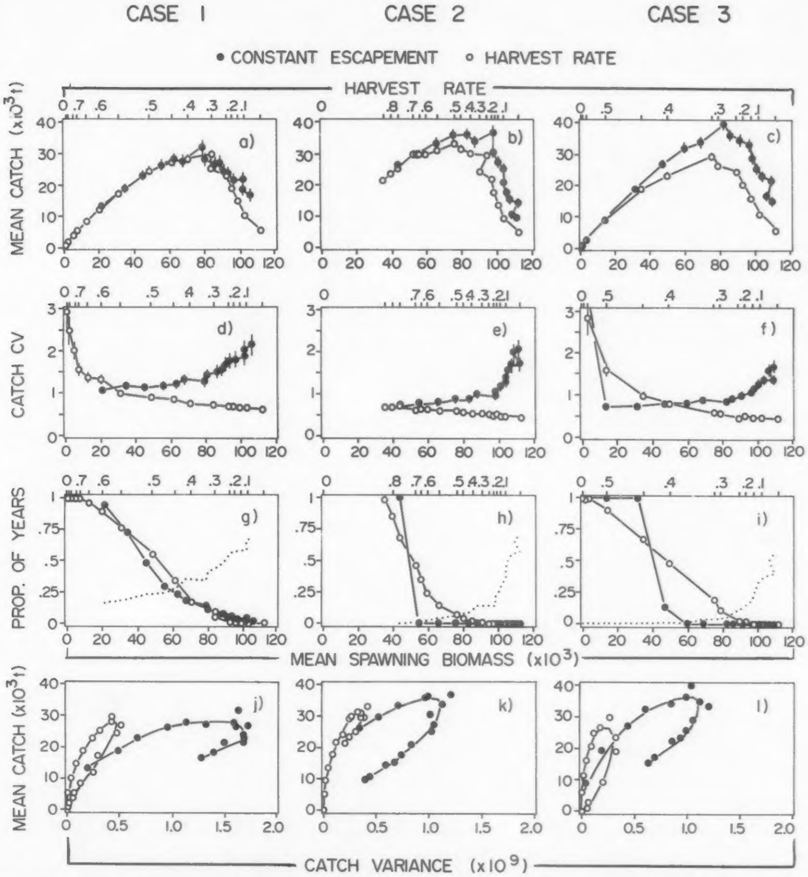

FIG. 5. Composite figure of the results of the model. Column 1 panels are from the basic model (random deviations). The panels in column 2 are from the model with correlated deviations. DFO's CUTOFF policy is compared in column 3. Row 1 is mean catch, row 2 is catch CV, row 3 is risk, and row 4 is mean/variance. The solid circles are the constant escapement strategy; the open circles are the harvest rate strategy. Along the top edge of most panels is a scale for the harvest rate (increments are not evenly spaced). This scale corresponds directly to the 17 harvest rate levels. The maximum values for the abscissa and ordinate scales are consistent between graphs. Catch CV and risk are unitless measures. Each point is the measured statistic (mean, CV, risk, variance) for 1500 simulated yr.

The following equations elaborate the above outline. The FORTRAN source code is listed in Hall (1986). The parameters of the model are presented in Table 2.

The model begins with a starting stock size at age 1 of 2 billion fish, the approximate mean N_1 since 1972 from VPA. Starting numbers for ages 2–10 are calculated by $N_a = N_{a-1}S_a$. The adult spawning biomass (tonnes) is

$$(8) \quad B_t = \sum_{a=1}^{10} N_{a,t} W_{a,t} P_{a,t}$$

where N_a is total number at age, W_a is weight at age, and P_a is the proportion of fish at age that are mature and spawning. The catch is subtracted from the spawning biomass (the harvest strategies that determine the catch are described below). The reproductive potential of the remaining spawning biomass is the number of eggs spawned:

$$(9) \quad \text{Eggs}_t = \sum_{a=1}^{10} N_{a,t} F_a \, 0.5.$$

The number of age 1 fish next year is determined by the stock–recruitment model (equation (4)). The age classes 2–10 are then updated, calculating backward from age 10 to age 2, by $N_a = N_{a-1}S_a$. The updated age classes are fed into equation (8) and the process repeats until the number of years that are being simulated are complete.

Stochastic variability is introduced in v_t by one of two methods. To simulate a random effect where the deviations in year t are independent from deviations in year t − lag (white noise), v_t is chosen from a normal random distribution, with mean 0, and standard deviation equal to the standard error of the regression residuals (equation (5)). The second method reflects the structure of the residuals in Fig. 3. The deviation in year t is dependent on the deviations in the previous years, plus an unpredictable random effect:

$$(10) \quad v_t = a_1 v_{t-1} + a_2 v_{t-2} + \text{normal deviate.}$$

The coefficients a_1 and a_2 were determined from autoregression of v_t on v_{t-1} and v_{t-2} (equation (5); Fig. 3). The order (number

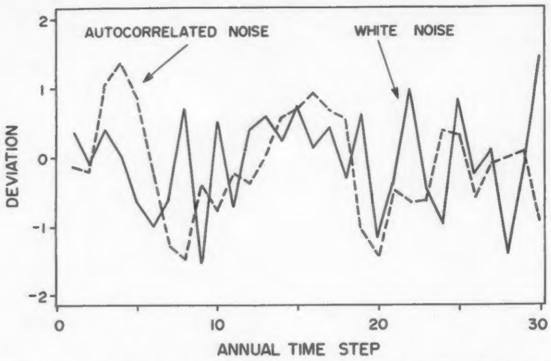

FIG. 6. Time series of simulated deviations showing the difference between random (white noise) and second-order correlated deviations. The correlated deviations show a rough periodicity, creating a platykurtotic distribution of deviations.

of lags) of the regression was determined by a computer program (C. J. Walters, pers. comm.) that locates the minimum Akaike criterion (Ulrych and Bishop 1975; Larimore and Mehra 1985); a second-order regression was selected by that criterion, with $a_1 = 0.945$ and $a_2 = -0.430$. Equation (10) is used in forward simulations by recursively updating the $v_{t-\text{lag}}$ deviations, beginning with $v_{-2} = -1.549$ and $v_{-1} = -0.880$, the residuals from 1981 and 1982.

Just as there are many alternatives for stock–recruitment models, there are an infinite number of hypotheses regarding population biology and population response to environmental change. To eliminate as much of the confounding effects of different population regulation mechanisms as possible, we chose to model the biology of the herring in its simplest form so that the effects of different harvesting strategies can be clearly shown. The age-specific biological parameters (mortality, maturity, fecundity, weight, and percent female) are assumed to be constant over time and population size. The stock–recruitment parameters (α, β, and v) are determined from historical data and remain constant. Recruitment variation follows two patterns: white noise and structured (autocorrelated) variation. The variation is not defined to be caused by species interactions, environmental effects, or other causes, although it may reflect any or all possibilities.

Harvest Strategies

We define a harvest strategy as a method of population removal that controls for population size and/or catch size. This definition distinguishes harvest strategies from harvest tactics. Harvest tactics are methods that management uses to implement a strategy. The different strategies that previous studies have used are (1) a proportion of the stock is removed, (2) stock size is controlled, (3) catch level is controlled, and (4) fishing effort is controlled.

This study is limited to categories 1 and 2. Preliminary analysis eliminated control of catch levels (quotas) as a viable option for British Columbia herring stocks. To sustain a true constant catch (zero variance) the annual yield had to be maintained at a level that drastically reduced the long-term average yield compared with other strategies. At catch levels approaching the average maximum sustainable yield, the strategy lost the appeal of low catch variance. Harvest strategies that attempt to control fishing effort are not considered. The combined characteristics of high catchability of herring and overcapitalization of the fishing fleet make the strategy of effort control impractical for British Columbia herring.

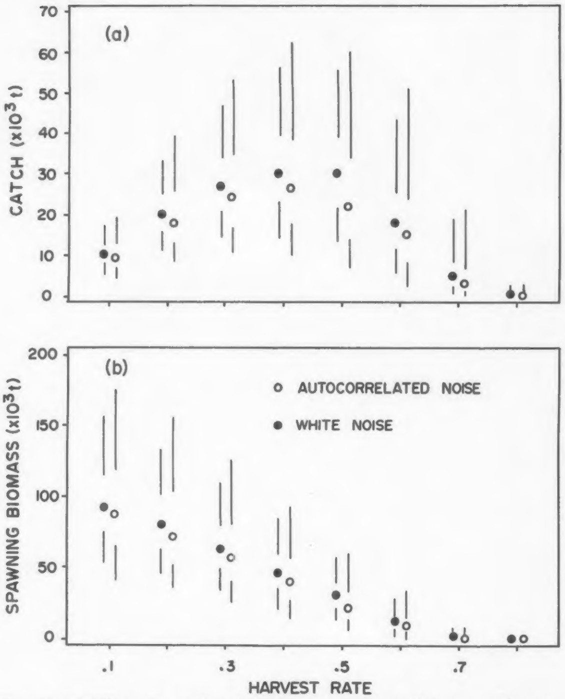

FIG. 7. (a) Effect of correlated deviations (open circles) on catch over a range of harvest rates versus the white noise model version (solid circles). The points are medians. Upper lines range from 75th to 95th quantiles; lower lines range from 25th to 5th quantiles. The distribution of catches from the model with correlated deviations (right point–line set) is more skewed and more disperse. (b) Effect of correlated deviations on spawning biomass. The spawning population shows increased skewness and dispersion with correlated deviations, the same effect as for catch (Fig. 7a).

For the following definitions "the population" refers to that part of the total population that has matured and is migrating to inshore spawning areas. This is the segment of the total population that is available for capture by the roe herring fishery. The term "constant" means that strategies do not change between years.

Harvest rate

The constant harvest rate strategy removes a fixed proportion of the population, $C = Np$, where p is the harvest rate. The remaining population ($N(1 - p)$) spawns.

Constant escapement

The constant escapement strategy controls for population size. A constant spawning biomass that is sufficient to sustain the population is determined. If the population is above the level required for the spawning biomass the surplus is removed as yield. If the population is below the spawning biomass requirement, no catch is removed from the population. This strategy is also known as a fixed escapement policy.

DFO's CUTOFF Policy

In 1985 the CUTOFF strategy was introduced as a safety measure to protect endangered stocks (M. Stocker[2]). The study calculates an unfished equilibrium biomass by simulation and graphical procedures based on a Ricker stock–recruitment relationship. The critical biomass is arbitrarily set at 25% of the unfished equilibrium, or 20 800 t for the combined Strait of Georgia and Johnstone Strait herring populations (M. Stocker[2]). The policy, which was in effect for the 1986 roe fishery, stipulates that no fishing will take place if the forecast population is below the critical stock biomass. At forecast stock sizes "marginally above" the CUTOFF level, the catch equals the forecast run minus the critical stock biomass. At stock sizes "well above" the critical level a 20% harvest rate is used.

The CUTOFF policy provides a method for a preseason justification of a fishing closure. The policy insures a stock buffer against over harvesting. It combines the safety of the constant escapement strategy and the catch variance reducing feature of the harvest rate strategy. To simulate the CUTOFF policy over a range of harvest rates and escapement goals, we used 20 800 t as the minimum spawning biomass. To insure that with harvesting the population never drops below this level, we define the upper boundary of the stock size region "marginally above" the CUTOFF level as the biomass that satisfies the inequality

$$(11)\quad \text{Stock} - (\text{harvest rate} \cdot \text{stock}) \leq \text{Critical biomass}$$

for the harvest rate strategy and

$$(12)\quad \text{Stock} - \text{escapement goal} \leq \text{Critical biomass}$$

for the constant escapement strategy. Stock sizes above the upper bound are harvested at the going rate.

Model Test Standards

The harvest rate strategy was tested at 17 harvest rate levels ranging from 0.05 to 0.85 in 0.05 increments. A zero harvest rate was included to measure unfished stock biomass.

The constant escapement strategy ranged from 7500 to 120 000 t in increments of 7500 t. Each strategy level was tested over 15 yr, after a 15-yr stabilizing period, during which no measurements were made. The 15-yr tests were repeated in 100 runs; for each policy level the total number of years was 1500.

Pseudo-random normal deviates (mean 0, standard deviation 1) were generated from a FORTRAN library subroutine. Mean and standard deviation were adjusted to suit particular distributions by the general formula ($D_{m,\mathrm{SD}} = \text{mean} + \mathrm{SD} \cdot D_{0,1}$.

Evaluation Criteria

To compare different harvest strategies, a set of evaluation criteria are needed. Following the pattern of other harvest strategy studies (see Hall 1986), we use mean catch as a primary criterion. Catch variance is measured for mean/variance tradeoff curves. The coefficient of variation of catch compares catch variance between different levels of the same harvest strategy and between different harvest strategies. Risk is measured by two criteria. The first is the risk of the stock size decreasing below a defined critical level, the usual risk of concern to management. Type 2 risk is that incurred by fishermen, the risk of zero allowable catch and no fishing. The following five specific criteria are used to compare the two strategies.

(1) Mean catch: the catch is summed for all years and runs for a given harvest strategy level and divided by the product of the number of years and runs:

$$(13)\quad \bar{C} = \sum_{k=1}^{\mathrm{NR}} \sum_{i=1}^{\mathrm{NY}} C_{i,k}/\mathrm{NY} \cdot \mathrm{NR}$$

where C is the catch, NY is the number of years, and NR is the number of runs.

(2) Catch variance:

$$(14)\quad \mathrm{Var} = \frac{\Sigma C^2 - ((\Sigma C)^2/N)}{N-1}$$

where ΣC is the sum of catch over all years (NY) and runs (NR), as in equation (13), and N is the product of NY and NR.

(3) Coefficient of variation of catch: the standard deviation of the catch is divided by the mean catch, $\mathrm{CV} = \sqrt{\mathrm{Var}}/\bar{C}$.

(4) Risk of subcritical stock size: the minimum spawning biomass is 20 800 t, approximately 25% of the unfished equilibrium biomass (M. Stocker[2]). The number of years in the simulation that the spawning biomass falls below this level are summed. The total is expressed as a proportion by dividing by N.

(5) Risk of no fishing: the number of years that catch is zero are summed and divided by N.

Results from three versions of the basic model are presented. The first version has recruitment variation controlled by independent random deviations (white noise). In the second version recruitment deviations are structured with autocorrelation. The third version considers DFO's CUTOFF policy of maintaining a minimum spawning biomass of 20 800 t with autocorrelated deviations.

Results and Discussion

Basic Model

The results are presented in Fig. 5. The first nine panels (Fig. 5a–5i) use mean spawning biomass as the coordinate measure for the abscissa. Spawning biomass is averaged over all years and runs of the model (similar to mean catch, equation (13)). Annual spawning biomass varies widely for the harvest rate strategy. For example, in Fig. 5a the 90% limits are 36 200 and 107 700 t for the 0.30 harvest rate. We emphasize this point to clarify the use of the figures. They are not intended as short-term management harvest guidelines. It is incorrect to say that if the forecast spawning biomass is 60 000 t, the expected catch is 28 000 t. It is correct to say that if the population is managed to maintain an average spawning biomass of 60 000 t, then the long-term average catch will be around 28 000 t.

The relationship between escapement levels for the constant escapement strategy and the mean spawning biomass (abscissa) is exactly proportional for low escapement goals. As the escapement goal increases above 20 000 t, the probability that the spawning biomass is less than the escapement goal increases.

White noise is the most common form of induced variation in harvest strategy models. Deviations from the recruitment function are modeled as independent and identically distributed variables. The constant escapement strategy provides significantly higher average catches over a wide range of stock sizes, but at the expense of increased variation in catch (Fig. 5a, 5d). High average catches for the constant escapement strategy result from this strategy capitalizing fully on large positive recruitment fluctuations that characterize clupeid fisheries. The relationship deteriorates at extreme stock levels. As escapement goals approach and exceed 80 000 t, the population is frequently unsuccessful at meeting the demand, and catch is zero for these years, lowering the mean catch and drastically increasing the catch variance for the constant escapement strategy. At low stock sizes, mean catch is the same for both strategies. Low stock sizes produce fewer recruits, and any large positive recruitment fluctuations are cropped as catch by high harvest rates and low escapement levels.

The difference between strategies is most apparent in the criterion of catch variance (Fig. 5d, 5e, 5f). For the harvest rate strategy, catch CV gradually increases with increasing harvest rates. As harvest rates increase above 0.60, catch more closely mimics the highly variable population fluctuations, increasing catch variance. The dampening effect of the spawning biomass absorbing population fluctuations is reduced. For the constant escapement strategy, all variation in population size is transmitted to the catch variance. Catch CV increases with escapement level, as the population becomes less likely to meet higher escapement goals.

Risk is measured as the proportion of years that the population falls below the minimum spawning biomass of 20 800 t (Fig. 5g, 5h, 5i). For the constant strategy, this measure is 1.0 for all escapement goals set below the critical level. As harvest rates increase above 0.45 the proportion of years that the spawning stock falls below 20 000 t increases rapidly. The third line (dotted) describes the risk of not fishing (Type 2). Type 2 risk affects only the constant escapement strategy, since the harvest rate strategy always removes some fish. As escapement levels become higher, the probability of meeting the goal decreases. Fishing is shut down in years of inadequate escapement. It is included on the figure as a reminder that the constant escapement strategy suffers from this additional element of risk.

Mean catch is plotted against catch variance (Fig. 5j, 5k, 5l) and a smoothed curve (Tukey 1977) is overlayed to define the mean/variance boundary region. The points are mean catch and catch variance for 1500 simulated yr for each strategy level (harvest rate 0.05–0.85 by 0.05 increments; constant escapement 7500–120 000 t by 7500-t increments). The curves tend to form a closed loop as harvest rates and escapement goals increase. The differences between the two strategies are striking. For a small sacrifice in mean catch, large gains can be made in reduced catch variance for the harvest rate strategy. For example, comparing maximum average yields and associated variances, a 78% reduction in catch variance can be achieved with only an 11% reduction in mean catch.

Correlated Deviations Model

Results from the version with correlated recruitment deviations are presented in Fig. 5, column 2. Description of results will concentrate on comparing versions of the model. The basic reasons for differences between strategies have been explained in the previous paragraphs. To reiterate the important points, (1) the constant escapement strategy provides higher average yields over a wide range of stock sizes, but at the expense of increased catch variation, (2) the harvest rate strategy reduces catch variance by transmitting inherent population variability to the spawning stock, and (3) the constant escapement strategy maintains higher average yields by fully utilizing large positive fluctuations in stock abundance. These qualitative results do not change for the other versions of the basic model, but the quantitative results do change.

Figure 5b shows that the difference between the strategies is greater because the mean catch at all stock sizes for the harvest rate strategy is significantly decreased. The explanation for the increased mean catch difference depends on understanding the processes of random versus serially correlated deviations and the resulting population structure. Figure 6 shows the two types of deviations for the same sequence of random normal deviates over a 30-yr period. The amplitude is almost the same, but there is ''periodicity'' in the correlated deviations. The effect is to ''spread out'' the deviations; there is a persistence to high and low deviations, with less clumping about the middle. The effect is transmitted to both catch and population size.

Figure 7 compares distributions for catch and spawning biomass for white noise and autocorrelated noise over a range of harvest rates. Both mean catch and mean spawning biomass are more dispersed under correlated deviations. Catch and population variance are increased. A side effect of increased dispersion in spawning biomass is reduced average recruitment compared with the white noise model. Spawning biomass is more often on the tails of the Ricker curve and less frequently in the more productive middle range. This produces a negative feedback on population size and lower average yields. Tautz et al. (1969) identified the detrimental effects of compensatory losses under a fixed percentage management scheme. Recruitment losses due to low spawning biomass are equally serious. The constant escapement strategy avoids this problem by fixing spawning biomass, reaping the benefits of persistent high recruitment and suffering no worse catches than the white noise model during lean years.

The pattern for catch variance for the white noise and the autocorrelated noise is similar. Catch CV for the correlated deviation model is about 30% higher over the range of harvest rates and 20–30% higher for the constant escapement strategy (Fig. 5d, 5e).

For the criterion of risk, the chance of the spawning stock dropping below 20 000 t increases slightly with correlated errors, since the spawning biomass varies more under a structured recruitment pattern (Fig. 5g, 5h). The difference in the mean/variance diagram is more pronounced (Fig. 5j, 5k). Catch variance for both strategies is doubled. For the same example cited in the previous section, an 18% catch reduction now reduces catch variance by 72%.

CUTOFF Model

Results from the CUTOFF policy are presented in Fig. 5, column 3. The spawning stock is not permitted to decrease below 20 800 t in any year. The first thought might be that this change in policy would tend to lower average yield, since in many years catch level will be reduced to maintain the minimum spawning biomass. Catch is reduced in many years, but the benefit of maintaining a minimum spawning reserve of 20 800 t is a long-term positive effect on mean catch. Under the CUTOFF policy, high harvest rates are not possible, since stock size is governed by the inequality (equation (3)) to never drop below 20 800 t. Above 0.30 the CUTOFF rule is effective. Actual harvest rates at strategy level objectives of 0.50 and 0.70 are 0.48 and 0.56. Above the CUTOFF level the curves are nearly identical to the correlated noise model.

The curves comparing the criterion of catch variance are also similar. The ascent of the harvest rate curve is held in check by the CUTOFF limit. For risk the curves are shifted slightly to the right as stock size nears the CUTOFF level. The grouping about the CUTOFF limit is clear in the mean/variance figure. This area of the graph highlights an interesting comparison between the strategies. It would seem that the strategies are almost equivalent at mean yields of about 30 000 t and variance about 4.0×10^8. However, by referring to the mean catch figure (Fig. 5c) to find the associated stock size (about 22 000 t) and then to the risk figure (Fig. 5i), this region is a location to avoid if we are concerned about the stock size falling below the critical limit. Away from this region the differences between the strategies provide clearer choices.

Conclusions

(1) The constant escapement strategy produces consistently higher average yields over a wide range of population sizes maintained by either constant escapement levels or constant harvest rates. The range of population sizes includes all realistic management options.

(2) Over the same range of population sizes, catch variance is significantly lower for the harvest rate strategy.

(3) The threat of the spawning population decreasing below a predefined critical level is greatest for high harvest rates. At harvest rates below 0.30 the probability is always less than 0.05.

(4) The risk of no fishing due to insufficient stock size is always lower, and usually zero, for the harvest rate strategy. The risk of no fishing increases as escapement goals increase for the constant escapement strategy. Strategy modifications that create a reserve spawning biomass further increase the probability of fishery closures under the constant escapement strategy.

(5) Serial correlation between deviations that determine recruitment success lowers average yields and increases catch variance for both strategies.

(6) Correlation between recruitment deviations and subsequent stock size causes bias in estimates of stock–recruitment parameters. The stock appears more productive than it really is.

Conclusions 1–4 are a function of how each strategy accommodates the natural population fluctuations characteristic of herring. The constant escapement strategy transmits all variation to the catch. This increases mean yield and catch variance as the constant stock strategy fully uses population surplus above the escapement requirement. The harvest rate strategy partitions the population variance between catch and spawning biomass, slightly reducing and greatly stabilizing yields.

Acknowledgments

Support was provided by a University of British Columbia Graduate Fellowship. Vivian Haist and Jake Schweigert kindly reviewed the manuscript.

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NOTES

Fatty Acid Composition in Eggs of Atlantic Cod (*Gadus morhua*)

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Ulvund, K. A., and O. Grahl-Nielsen. 1988. Fatty acid composition in eggs of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 45: 898–901.

Fatty acids were determined in single eggs of Atlantic cod (*Gadus morhua*). The eggs were obtained a few hours after spawning and fertilization from 4-yr-old cod kept in aquaria. By multivariate treatment of the analytical results, the composition of fatty acids was found to vary between eggs within the same spawning batch from the same female. A different variation was found between eggs from the first spawning batch from two different females. The two females had been reared under identical conditions from the egg stage, but were of different sizes at the time of spawning. The fatty acid content in the eggs from the smallest was 4% lower than in the largest. Eggs from the eighteenth spawning batch contained 23% less fatty acids than those from the first batch from the same female. The decrease differed between the acids: the monoenic acids had decreased by 29%, the polyunsaturated acids by 26%, and the saturated acids by 9%.

Les auteurs ont mesuré les acides gras dans des oeufs de morue de l'Atlantique (*Gadus morhua*) pris un par un. Les oeufs ont été recueillis quelques heures après la ponte et la fécondation; les poissons étaient des morues de 4 ans gardées en aquarium. Après traitement des résultats de l'analyse avec plusieurs variables, on trouve que la composition des acides gras varie d'un oeuf à l'autre au sein de la même ponte d'une même femelle. On observe une variation différente entre les oeufs de la première ponte de deux femelles différentes. Les deux femelles avaient été élevées dans des conditions identiques depuis le stade de l'oeuf, mais étaient de tailles différentes au moment de la ponte. La proportion d'acides gras dans les oeufs de la femelle la plus petite était de 4 % inférieure à celle relevée chez la plus grosse. Les oeufs de la 18ᵉ ponte contenaient 23 % de moins d'acides gras que la première ponte de la même femelle. La diminution n'était pas la même pour tous les acides : les monoinsaturés avaient baissé de 29 %, les polyinsaturés de 26 % et les saturés de 9 %.

Received August 5, 1987
Accepted January 25, 1988
(J9381)

Reçu le 5 août 1987
Accepté le 25 janvier 1988

Several investigations have been concerned with the requirements of fatty acids in the eggs of fish. For freshwater fish, egg quality, measured as hatchability and other parameters, has been related to the content of fatty acids in the eggs (Watanabe et al. 1984). The importance of fatty acid 22:6 (*n*–3) was shown, but this may possibly be replaced by 20:4 (*n*–6). (In the shorthand nomenclature of the fatty acids, the first number indicates the number of carbon atoms, the number after the colon indicates the number of double bonds, and the position of the double bonds is denoted by (n-*x*) where *n* is the chain length and *x* is the number of carbon atoms from the last double bond to the terminal methyl group.) For marine fish, it has been deduced from the high content of *n*–3 polyunsaturated fatty acids in eggs and larvae that these acids are required for successful development (Tocher and Sargent 1984; Tocher et al. 1985). An essential role of 20:4 (*n*–6) has also been postulated, due to the unique and consistent fatty acid composition of phosphatidylinositol at the earliest stage of the fishes' life history (Tocher and Sargent 1984).

Atlantic cod (*Gadus morhua*) is of particular interest due to intensive commercial fisheries and also due to the promising outlook for culturing this species (Øiestad et al. 1985). Cod has a spawning period which lasts for 1–2 mo, during which discrete batches of eggs are spawned every 2–3 d. A similar spawning pattern has been shown for haddock (*Melanogrammus aeglefinus*) (Hislop et al. 1978). The size of the eggs decreases during the spawning period (Sivertsen 1935). It has also been shown that various parameters, such as weight, length, myotome height, and gape of the mouth, of 5-d-old larvae of cod correlate with the dry weight of the eggs (Knutsen and Tilseth 1985).

The fatty acid composition of cod roe has been determined by Tocher and Sargent (1984). Possible variations due to time of spawning were not considered. Nor were variations between individual females, or between individual eggs, discussed. However, influence of parental diet on the composition of the lipids in eggs was suggested. Dependence on the parental diet of the fatty acid composition in the eggs of rainbow trout (*Salmo gairdneri*) was demonstrated by Watanabe et al. (1984).

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A method for chemometric determination of fatty acids in single eggs has been developed in our laboratory (Grahl-Nielsen and Barnung 1985; Barnung and Grahl-Nielsen 1987). This allows statistical retrieval of information from the total fatty acid pool of the eggs.

An extensive experiment with spawning cod in aquaria was carried out at the Institute of Marine Research during the winter and spring of 1987 (O. S. Kjesbu, Institute of Marine Research, P.O. Box 1870, N-5024 Bergen, Norway, pers. comm.). Eggs from different spawning batches from individual females were available from this experiment.

With proper samples of eggs available and an analytical method at hand, the purpose of the present investigation was to determine the variation in fatty acid composition between individual eggs from the same female, between eggs from different females of the same year-class, and between different spawning batches from the same female.

Materials and Methods

The cod used in this project were reared at the aquaculture station at Austevoll. Fertilized eggs were collected from a group of cod in a sea-cage in the winter of 1983. After the eggs had hatched in aquaria, the larvae were released to a saltwater pond (Øiestad et al. 1985). At the end of the first year, they were transferred to a sea-cage where they were kept and fed for 3 yr. They were then transferred to aquaria at the Institute of Marine Research, one female and two males in each aquarium. As the spawning started at the beginning of February 1987, the cod stopped eating (O. S. Kjesbu, pers. comm.). Immediately after each batch of eggs was spawned/fertilized and swelled, the eggs were collected from the surface with a sieve. Single eggs were transferred to 4 × 150 mm ampoules with 200 μL of anhydrous methanol containing 2 N HCl and the four fatty acids 15:0, 17:0, 21:0, and 23:0 as internal standards. The ampoules were sealed and heated at 100°C for 6 h. The ampoules were opened and the methanol was evaporated by N_2 gas down to approximately 50 μL. An equal amount of water was added and the water–methanol phase was extracted twice with 350 μL of hexane. The combined extracts were evaporated by N_2 gas down to 40 μL. One microlitre was chromatographed on a 30 m × 0.32 mm fused silica column (J&W Scientific, Inc.) with 50% cyanopropylmethyl-(50%)-methylphenylpolysiloxane, of 0.25 μm thickness, as the stationary phase and helium as the mobile phase. The column was mounted in a Hewlett-Packard 5890 gas chromatograph with on-column injection and a 1 m × 0.53 mm empty, deactivated precolumn and flame-ionization detection. The sample was injected at 130°C, and the oven temperature was then raised at 3°/min to 210°C, where it was left isothermal. The detector output was coupled to a VG Multichrome lab-data system for storage and treatment of the chromatograms. The areas of the peaks were integrated and converted to weights by way of the internal standards, using the

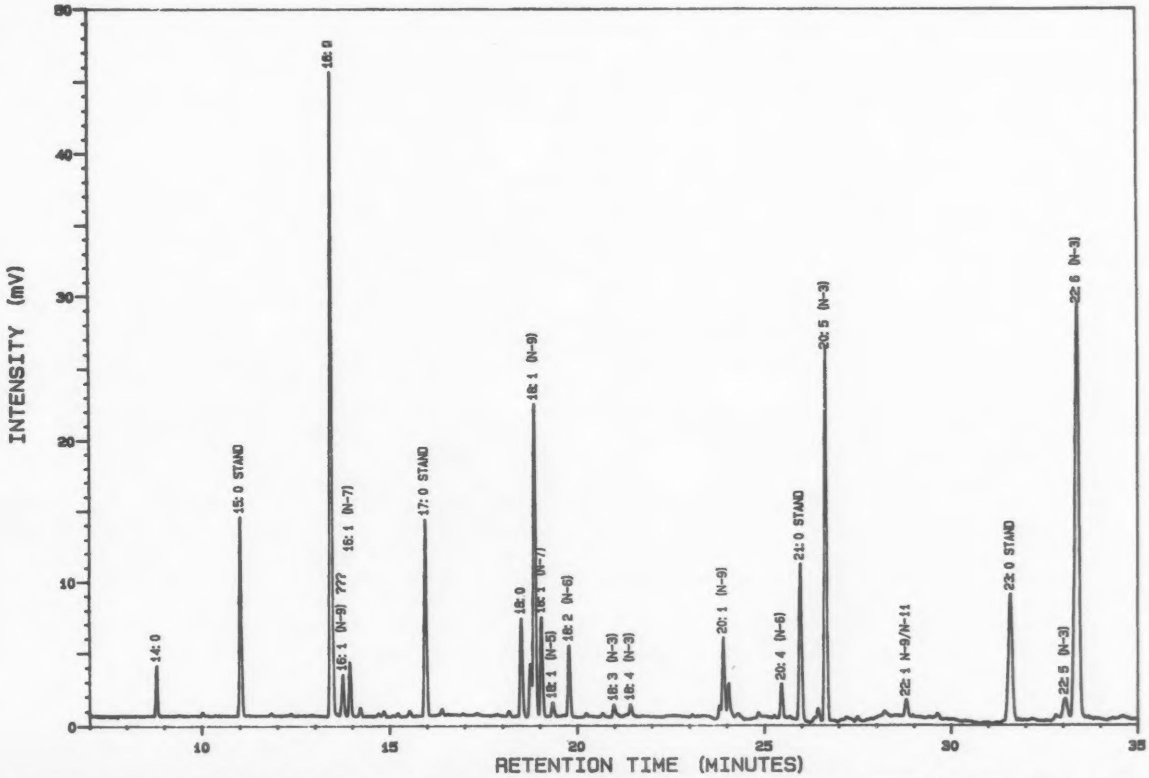

FIG. 1. Gas chromatogram of fatty acids, as methyl esters, from a cod egg. The 17 identified components were used for multivariate data analysis.

TABLE 1. Relative fatty acid composition, as a percentage of total, in eggs from the first and eighteenth spawning batch from one cod and from the first spawning batch of another cod, as well as the difference in absolute amounts between the two batches from the first cod and the difference between the first batches from the two cods.

Fatty acid	Cod 1		Cod 2, batch 1[b]	Cod 1 (% reduction)[c]	Cod 1 − Cod 2 (% difference)[d]
	Batch 1[a]	Batch 18[b]			
14:0	1.4±0.05	1.5±0.1	1.4±0.2	16.6	+1.0
16:0	20.3±0.4	25.2±0.9	19.9±0.8	4.0	−6.2
16:1 (*n*–9)	1.5±0.06	1.5±0.05	1.4±0.06	22.0	−7.8
16:1 (*n*–7)	1.7±0.04	1.7±0.05	1.8±0.1	25.0	+2.8
18:0	3.4±0.2	2.7±0.08	3.6±0.2	38.1	+2.2
18:1 (*n*–9)	13.0±0.3	12.4±0.3	12.4±0.5	26.4	−8.6
18:1 (*n*–7)	4.1±0.4	3.6±0.1	4.0±0.4	31.6	−6.1
18:1 (*n*–5)	0.5±0.07	0.4±0.03	0.6±0.08	43.8	+13.2
18:2 (*n*–6)	2.5±0.1	2.4±0.05	2.5±0.1	25.6	−3.4
18:3 (*n*–3)	0.4±0.03	0.4±0.02	0.4±0.02	29.7	−2.0
18:4 (*n*–3)	0.5±0.03	0.4±0.04	0.6±0.04	43.8	−1.2
20:1 (*n*–9)	3.7±0.2	3.1±0.1	3.7±0.2	36.5	−3.7
20:4 (*n*–6)	1.2±0.09	1.3±0.03	1.4±0.1	19.3	+7.7
20:5 (*n*–3)	14.2±0.7	14.1±0.3	15.0±0.7	23.1	+0.9
22:1 (*n*–11)	0.8±0.3	0.7±0.03	0.8±0.1	34.3	+3.3
22:5 (*n*–3)	1.3±0.2	1.7±0.3	1.2±0.2	1.4	−13.1
22:6 (*n*–3)	29.5±1.6	27.1±0.5	29.2±1.7	28.8	−5.1
Saturates	25.0	29.4	24.9	9.2	−4.6
Monounsaturates	25.3	23.2	24.9	29.0	−5.8
Polyunsaturates	49.7	47.4	50.2	26.2	−3.2
Total				22.7	−4.2

[a] Average and standard deviation of the analyses of seven eggs.

[b] Average and standard deviation of the analyses of nine eggs.

[c] Percent reduction from batch 1 to batch 18 of the absolute amounts of the fatty acids.

[d] Percent difference between the first batches from cod 1 and cod 2 of the absolute amounts of the fatty acids.

same reponse factor for all fatty acids. It was not experimentally shown that all fatty acids indeed had the same analytical response. However, possible errors in absolute amounts will not influence the results of the present investigation, where comparison between samples is the objective.

The relative amounts of 17 fatty acids in 25 analysed eggs were subjected to principal component analysis using the program SIMCA (Kvalheim 1985). In this, the 25 samples were placed in a 17-dimensional space, i.e. with one coordinate for each of the 17 fatty acids. The dimensionality was then reduced from 17 to the 2 that represented the directions of the largest and second largest variation of the samples in the original coordinate system.

Results and Discussion

A typical chromatogram of the fatty acid methyl esters from a cod egg is shown in Fig. 1. Peaks in the chromatogram were identified by comparison with chromatograms of standrds. In this manner, 17 fatty acids, from 14:0 to 22:6 (*n*–3), have been identified. They were found in all eggs, and their relative amounts were expressed as a percentage of the total amount of fatty acids (Table 1).

The variation in fatty acid composition between the different eggs from the same batch, indicated in the principal component plot in Fig. 2, is obvious. This substantiates our earlier observation on variation between individual eggs from the same female (Barnung and Grahl-Nielsen 1987). Such differences between eggs are not detected in the common methods of determination of fatty acids, where a large number of eggs are pooled for each analysis.

The eggs from the two female cod were different (Table 1). The two cod had been reared under identical conditions, but were of different size, the larger weighing 4.2 kg and measuring 64 cm and the smaller weighing 2.8 kg and measuring 56 cm as determined 2 mo before spawning started. The total amount of fatty acids was 4.2% lower in the eggs from the smaller cod. The difference was not the same for all the fatty acids; in fact, some were present in higher amounts in the eggs from the smaller cod. This resulted in a separation of the two groups along the second principal component (Fig. 2). The variance between the eggs within each group, which apparently is larger than the variance between the groups, is greatest along the first principal component. This means that the fatty acids responsible for the difference between the females are not the same as those responsible for the difference within the females. One of the advantages of the multivariate analysis is that it is able to distinguish between different variances.

The largest observed differences were between the eggs from the first and the eighteenth spawning batch from the same cod (Table 1; Fig. 2). In the last batch the total amount of fatty acids was almost one fourth lower than in the first whereas the reduc-

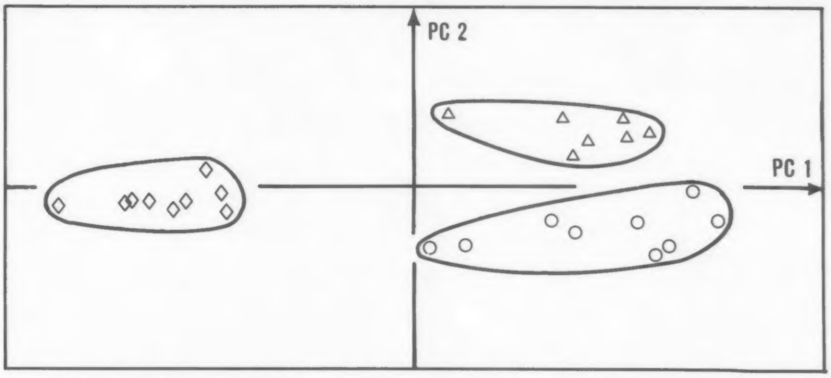

FIG. 2. Principal component (PC) plot of cod eggs. Triangles and diamonds, respectively, represent eggs from the first and eighteenth batch from the first female and circles represent eggs from the first batch from the second female. The first PC accounts for 93.6% of the total variation and the second PC accounts for 2.9%.

tion of the individual fatty acids varied between 1% and more than 40%.

The present investigation shows that the fatty acid composition in the eggs changes within and between females. In addition to the sources of variation demonstrated here, which were weight of female and egg batch within a female, other sources are likely, e.g. differences in the age of the females. The female diet is probably also important, as suggested by Tocher and Sargent (1984), and shown for rainbow trout by Watanabe et al. (1984). If at all accessible, a "typical" composition of the fatty acids of eggs of each species of fish therefore will have broad limits, and this has to be taken into consideration in comparison between eggs from different species.

The main question is, however, which consequences these differences might have for successful development of the eggs and larvae. Since it has been suggested that the composition of fatty acids in the ripe eggs is important for the development of the early life stages of marine fish (Tocher et al. 1985), it is reasonable to believe that the lower supply of fatty acids, the unsaturated in particular, in the eggs from the eighteenth spawning batch, as compared with those from the first batch, will influence the quality of the eggs. We are currently conducting a more thorough investigation on the variation of the fatty acid composition in eggs from various sources. This will be succeeded by a study of the biological significance of the differences.

Acknowledgments

We are grateful to O. S. Kjesbu and P. Solemdal, Institute of Marine Research, for the supply of well-defined cod eggs.

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Juvenile Atlantic Cod (*Gadus morhua*) Can Be More Freeze Resistant than Adults[1]

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Kao, M. H., and G. L. Fletcher. 1988. Juvenile Atlantic cod (*Gadus morhua*) can be more freeze resistant than adults. Can. J. Fish. Aquat. Sci. 45: 902–905.

Adult Atlantic cod (*Gadus morhua*) produce antifreeze glycopeptides during the winter which help to depress the freezing point of their blood plasma to approximately −1.2°C. Since the temperature at which fish can freeze and die approximates the freezing point of their blood plasma, it is evident that adult cod do not have the capacity to survive in ice-laden waters when the water temperatures drop to −1.5°C. Templeman and Fleming hypothesized that small cod are more adapted to cold water than adults. The present study documents the fact that the blood plasma freezing points of juvenile cod (mean length = 33 cm, 3-yr-olds) were significantly lower than those of adult cod (>45 cm) (juvenile, −1.55 °C; adult, −1.23°C). This difference was largely attributable to the doubling of plasma antifreeze glycopeptide levels in the juvenile cod. These results directly support Templeman and Fleming's hypothesis and indicate that juvenile cod, unlike adults, are capable of surviving the icy marine conditions which prevail along the northeast coast of Newfoundland during the winter.

La morue de l'Atlantique (*Gadus morhua*) adulte produit des glycopeptides antigels pendant l'hiver pour abaisser le point de congélation du plasma sanguin jusqu'à environ −1,2°C. Étant donné que la température à laquelle le poisson peut geler et mourir s'approche du point de congélation de son plasma sanguin, il est évident que la morue adulte ne peut pas survivre dans les eaux glacées quand la température de l'eau atteint −1,5°C. Templeman et Fleming ont déjà formulé l'hypothèse que les petites morues sont mieux adaptées aux eaux froides que les adultes. La présente étude fournit des preuves que le point de congélation du plasma sanguin de morues juvéniles (longueur moyenne = 33 cm, 3 ans) est nettement inférieur à celui de morues adultes (>45 cm) (juvénile, −1,55°C; adulte, −1,23°C). Cette différence est en grande partie imputable au doublement des niveaux de glycopeptide antigel dans le plasma des morues juvéniles. Ces résultats étayent directement l'hypothèse de Templeman et Fleming et révèlent que les morues juvéniles, au contraire des adultes, sont capables de survivre dans les eaux glacées qui prédominent le long de la côte nord-est de Terre-Neuve pendant l'hiver.

Received July 23, 1987
Accepted February 12, 1988
(J9367)

Reçu le 23 juillet 1987
Accepté le 12 février 1988

During the winter months the solute concentration (termed colligative properties) of Atlantic cod (*Gadus morhua*) plasma depresses its freezing point to approximately −0.75°C. Since Newfoundland winter water temperatures can decline to −1.4 to −1.8°C, it is evident that cod residing in these waters can be supercooled by almost 1° (Fletcher et al. 1982). This condition would be lethal to most fish if they should come into contact with ice (Scholander et al. 1957). However, Atlantic cod survive this potential danger by producing plasma antifreeze glycopeptides (AFGP) which noncolligatively depress the serum freezing point to safe levels (Hew et al. 1981). These antifreezes are 200–300 times more effective in lowering the freezing point than any other known proteins (DeVries 1983).

We have been studying the environmental factors controlling the seasonal cycle of AFGP in cod for the past 7 yr (Fletcher et al. 1987). During this time it became obvious that although AFGP gave cod increased freezing resistance over that conferred by the plasma electrolytes, it was not sufficient to protect them from freezing when the water temperatures declined below approximately −1.2°C. Although this limited degree of freeze protection called into question the functional significance of AFGP in cod, it was accepted that some degree of freeze protection was better than none.

Some years ago, Templeman and Fleming (1965) expressed the opinion that small cod were more adapted to cold water than

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[1] Contribution No. 714 of the Marine Sciences Research Laboratory.

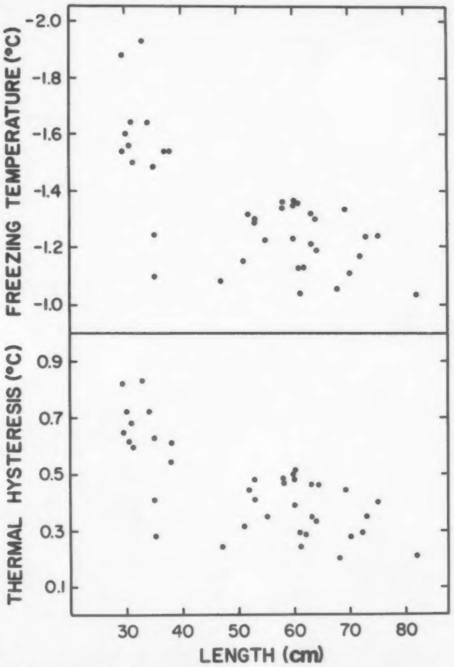

FIG. 1. Relationship between plasma freezing temperature, thermal hysteresis, and body length in Atlantic cod. All fish were blood sampled on March 6, 1987. Water temperature was −1.2°C. Each point represents an individual fish.

adults. We had not had the opportunity to test this supposition until the past winter (1986–87). The present study provides evidence that young cod are more adapted to icy waters than are adults by virtue of their higher plasma antifreeze levels.

Materials and Methods

Atlantic cod were caught in traps in Conception Bay, Newfoundland, during the summer and early fall. At the laboratory they were maintained in a 40 000-L seawater (32‰) aquarium under seasonally ambient conditions of water temperature and photoperiod (see Fletcher 1977) and fed capelin (*Mallotus villosus*) several times each week.

Blood samples (1 cm^3) were taken on March 6, 1987 (approximate time of peak plasma antifreeze levels), from a caudal blood vessel using plastic 3-cm^3 syringes equipped with 21-gauge needles and heparinized in Vacutainers containing sodium heparin (Becton Dickinson). The red cells were removed from the plasma by centrifugation (4000 × *g*). The total length of each fish was measured to the nearest 0.5 cm.

Plasma freezing and melting points were determined using a Nanolitre osmometer (Clifton Technical Physics, Hartford, NY). In this method the melting and freezing behavior of a small ice crystal is observed under a microscope under controlled temperature conditions. Thermal hysteresis, a measure of antifreeze activity, is the difference between the freezing and melting temperatures (Kao et al. 1986).

Plasma Cl^- was determined coulometrically using a chloride titrator (model CMT 10, Radiometer Copenhagen). Statistical comparisons between groups were carried out using Student's *t*-test (Snedecor and Cochran 1967).

Antifreeze glycoproteins were purified by trichloroacetic acid precipitation followed by gel filtration chromatography. An equal volume of 20% trichloracetic acid was added directly to the plasma (1.9 mL). Following low-speed centrifugation, the acid-soluble materials were desalted on a Sephadex G25 column (1.5 × 90 cm) in 0.1 M NH_4HCO_3 (pH 8.0). The materials coming out of the void volume were lyophilized, redissolved in 1.0 mL of 0.1 M NH_4HCO_3 (pH 8.0), and rechromatographed on a Sephadex G75 column (0.9 × 60 cm). Each fraction collected was lyophilized, redissolved in 0.3 mL of 0.01 M NH_4HCO_3, and their antifreeze activity (thermal hysteresis) determined.

According to Fleming (1960), cod of 30–40 cm (total length) are approximately 3 yr old and sexually immature. In this note, these cod are termed juveniles.

Results

The plasma from 11 of the 13 juvenile cod sampled had lower freezing temperatures and greater antifreeze activity (thermal hysteresis) than any of the adult cod (>40 cm) (Fig. 1). Mean plasma freezing temperatures of juvenile cod were significantly lower (by 0.32°) than those of adults (Table 1). These lower freezing temperatures in the juveniles were largely (80%) attributable to their greater levels of antifreeze glycopeptide activity. However, the small but significant difference in the melting temperature indicates that the lower freezing temperatures were also due in part to increased concentrations of dissolved solutes (Table 1).

Column chromatography (Sephadex G75) of the acid-soluble antifreeze glycopeptides from juvenile and adult cod revealed the presence of one major component containing antifreeze activity. Since the same volume of plasma (1.9 mL) was used for both groups of cod, it is apparent that the greater antifreeze activity observed in juvenile cod is attributable to increased amounts of this major antifreeze component (Fig. 2).

The juvenile cod plasma also contained some minor antifreeze components (fractions 18–26, Fig. 2) which were not evident in the adult cod plasma samples used. This difference is probably due to the relatively low concentrations of total antifreeze proteins in the adult cod. Previous studies have demonstrated the presence of these minor components when larger plasma volumes were used (Hew et al. 1981).

We have been collecting data on adult cod (>50 cm) plasma antifreeze activities for the past 7 yr (Fletcher et al. 1982, 1987). The frequency distributions of plasma antifreeze activity and plasma freezing point depression for all of the cod sampled during March (1981–87) and for the juvenile cod sampled in the present study are illustrated in Fig. 3. These data indicate that 70% of the juveniles sampled had a greater freezing point depression and greater amount of antifreeze activity than any of the adult cod sampled over the past 7 yr.

Discussion

The temperature at which ectothermic fish freeze and die closely approximates the freezing point of their blood plasma (Brett and Alderdice 1958; DeVries and Lin 1977; DeVries 1980; Fletcher et al. 1986). In most fishes the freezing point of plasma is determined by its colligative properties, the concentration of dissolved solute particles. The higher the concentration of dissolved solutes, the lower the freezing point is depressed below 0°C. Na^+ and Cl^- are the major dissolved solutes in plasma and account for 80–90% of the freezing point

TABLE 1. Comparison of the plasma freezing characteristics of juvenile and adult Atlantic cod. Juvenile cod were less than 40 cm in length. Antifreeze glycoprotein protein concentrations were estimated from the relationship between thermal hysteresis and antifreeze glycopeptide concentration (Fletcher et al. 1987). All values are expressed as means ± 1 SE. *P* is the level of statistical significance between juvenile and adult values.

	Length (cm)	Weight (g)	Cl (mM)	Freezing temp. (°C)	Melting temp. (°C)	Thermal hysteresis (°C)	Antifreeze glycoprotein (mg/mL)
Juvenile	33.0±0.8	316±3.2	196±2.4	−1.55±0.06	−0.929±0.023	0.625±0.042	13.7±1.19
Adult	62.0±1.6	2290±208	190±1.8	−1.23±0.02	−0.852±0.004	0.375±0.019	6.78±0.44
P	<0.001	<0.001	N.S.	<0.001	<0.01	<0.001	<0.001

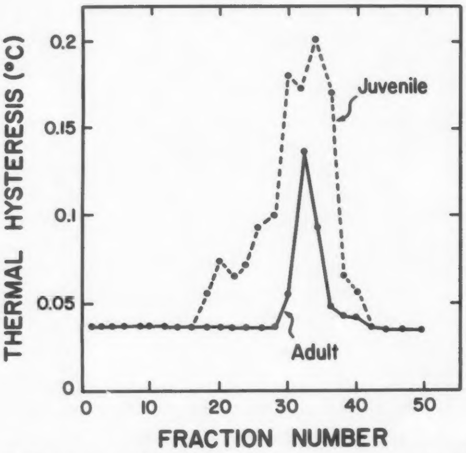

FIG. 2. Comparison of the elution profiles of Atlantic cod antifreeze proteins on Sephadex G75. Acid-soluble proteins were desalted on a Sephadex G25 column. The proteins were then rechromatographed on a Sephadex G75 column (0.9 × 60 cm). Individual fractions were lyophilized and redissolved in 0.01 M NH_4CO_3 and their freezing and melting points determined. Thermal hysteresis is the difference between the freezing and melting temperatures and is a measure of antifreeze activity.

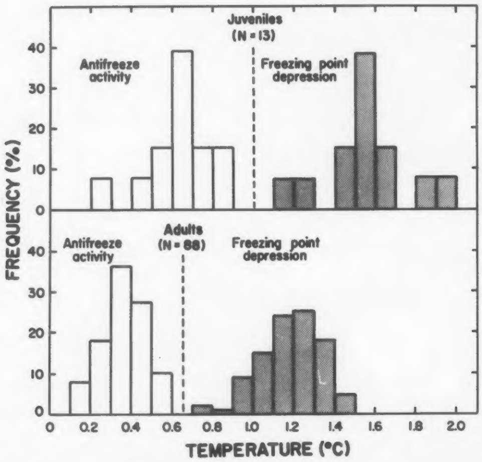

FIG. 3. Frequency distributions of plasma freezing point depression and antifreeze activity in juvenile and adult Atlantic cod. Data for the juvenile cod are from the present study. Data for the adults are compiled from blood samples collected during March from 1981 to 1987.

depression. The remaining 10–20% is due to other solutes such as K^+, Ca^{2+}, glucose, and amino acids (Holmes and Donaldson 1969).

The colligative properties of most teleosts' blood plasma give only a limited degree of freeze protection (−0.6 to −0.8°C). Thus in order to survive in icy marine waters where water temperatures can decline to approximately −2°C, a number of fish have evolved a set of antifreeze peptides or glycopeptides which depress the plasma freezing point below that caused by all of the other dissolved solute particles (DeVries 1983; Hew and Fletcher 1985; Scott et al. 1986). Intraperitoneal injections of antifreeze peptides into rainbow trout (*Salmo gairdneri*), which do not normally possess these peptides, increased their freezing resistance in direct proportion to the plasma antifreeze levels attained (Fletcher et al. 1986). Thus, antifreeze peptides appear to be directly responsible for the ability of marine teleosts to survive icy seawater at temperatures below the colligative freezing points of their blood.

The mechanism by which the peptide antifreezes inhibit freezing is not well understood. However, it appears that they bind to the surface of ice crystals and thereby prevent the addition of water molecules to the ice lattice (Raymond and DeVries 1977; Kao et al. 1986; Feeney et al. 1986; Yang et al. 1987).

The present study demonstrates that juvenile cod (3-yr-olds) had lower plasma freezing temperatures than adults and that these reduced freezing temperatures were almost entirely due to a doubling of antifreeze glycopeptide levels. Since the lethal freezing temperature of fish is directly related to the plasma freezing temperature, it is evident that juvenile cod can be more freeze resistant than adults. Indeed it appears that juvenile cod, unlike adults, are capable of surviving the icy marine conditions which prevail along the northeast coast of Newfoundland during the winter. Thus, Templeman and Fleming's (1965) hypothesis that small cod are more adapted to very low temperatures appears to be confirmed.

Do the differences in freeze resistance between juvenile and adult cod have a functional significance? Are juvenile cod more likely to encounter ice at water temperatures of −1.5°C than adults?

Our current knowledge of the migrations of "northern" cod has been summarized by Templeman (1979) and Lear and Green (1984). Briefly, the evidence indicates that in northeastern Newfoundland (Northwest Atlantic Fisheries Organization (NAFO) Division 3K), spawning occurs (March–June) in relatively deep (>250 m) and warm (3°C) waters on the outer continental slopes, or deep channels closer to the coast. The fertilized eggs then rise closer to the surface waters where they, along with developing larvae and fry, are transported southward and shoreward by the Labrador current. Many larvae then develop into juveniles in the shallow waters of bays and inlets of eastern Newfoundland (Lear and Wells 1984; Keats et al. 1987). These juvenile cod are believed to grow to sexual maturity ($\sim$5 yr) in inshore areas, residing in shallow water in summer and deeper water during winter (Fleming 1960; Templeman and Fleming 1965; Templeman 1979; Keats et al. 1987). The migration habits of adult cod differ appreciably from those of juveniles, for although they move to coastal waters around June, they migrate offshore again in October to the deeper, warmer waters of the spawning grounds (Templeman 1979).

It is evident from the foregoing paragraph that the migration habits of adult "northern" cod would normally prevent them from coming into contact with ice at subzero temperatures. Since water temperatures of 1°C and lower are necessary for antifreeze glycopeptides to be produced by cod (Fletcher et al. 1987), it would appear that adult cod inhabiting waters warmer than 1°C never synthesize antifreezes. However, some cod may not conform to the described migration patterns and be exposed to cold ($<$1.0°C) winter water. Such cod with their limited production of antifreeze would be protected down to temperatures of approximately −1.2°C. This level of freezing resistance would play a role in the survival of cod which are at risk of coming into contact with ice during early winter or late spring.

There appears to be little published evidence as to the whereabouts of juvenile cod during the winter. Templeman and Fleming (1965) found numerous small cod ($<$30 cm) and very few adults in St. Mary's Bay, Nfld., throughout the winter. However, although these fish were in cold water (−1.4°C), they were also too deep ($>$100 m) to be exposed to ice. Our knowledge of these juvenile cod is too limited to know whether or not they occasionally move into shallower icy waters. Small numbers of very young cod ($\sim$1 yr) have been found during the winter in the shallow waters (1 m) of Bellevue Beach, Trinity Bay, Nfld. (D. Methven, unpubl. data). Thus, juvenile cod may run a greater risk of encountering ice at very low temperatures than adults.

We know very little about the mechanisms regulating plasma antifreeze levels in fish. Thus, the reasons, physiological or biochemical, why the juvenile cod in this study had twice the amount of antifreeze found in adults must await further experimentation. However, since the offshore migrations to deep warm water, where the fish are safe from freezing, appears to be related to sexual maturation, one obvious hypothesis to test is whether the decline in plasma antifreeze levels in adults is related to changes in reproductive hormones.

Acknowledgements

We would like to thank Don Clark for the use of his juvenile cod and Alice Cadigan and Madonna King for their assistance. This research was supported by the Natural Sciences and Engineering Research Council of Canada.

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Wind-Aided Recruitment of Canadian Arctic Cisco (*Coregonus autumnalis*) into Alaskan Waters

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Summer wind data collected at Barter Island, Alaska, were compared with commercial fishery catches of arctic cisco (*Coregonus autumnalis*) at the Colville River, Alaska, for the period 1967–85. There was a significant ($p = 0.036$) association between yearly catch-per-unit-effort and the percent of easterly winds after adjusting for a 5-yr differential in the two time series. Results suggest that young-of-the-year fish which spawn in Canada's Mackenzie River are aided in their westward dispersal into Alaskan waters via wind-driven longshore currents. The greater the prevalence of easterly winds (westerly currents), the greater the recruitment. Increased recruitment manifests itself as an increase in Alaskan commercial fishery catch some 5-yr later when fish have grown to a size that renders them susceptible to commercial nets.

On compare les données sur le vent recueillies en été à l'île Barter (Alaska) aux données sur les prises commerciales de cisco arctique (*Coregonus automnalis*) dans la rivière Colville (Alaska) pour la période 1967–1985. Il existe un rapport significatif ($p = 0{,}036$) entre les prises annuelles par unité d'effort et le pourcentage de vent d'est quand on tient compte d'une différence de 5 a dans les deux séries temporelles. Les résultats portent à croire que les courants de vent côtiers aident les jeunes de l'année qui fraient dans les eaux canadiennes du fleuve Mackenzie dans leur dispersion vers l'ouest dans les eaux de l'Alaska. Plus la fréquence des vents d'est (courants d'ouest) est élevée, plus le recrutement est élevé. Un recrutement amélioré se manifeste par une augmentation des prises commerciales en Alaska quelque 5 a plus tard quand les poissons ont atteint une taille les rendant vulnérables aux filets commerciaux.

Received September 1, 1987
Accepted November 12, 1987
(J9408)

Reçu le 1 septembre 1987
Accepté le 12 novembre 1987

The arctic cisco (*Coregonus autumnalis*) is one of the most abundant anadromous fishes found in coastal waters of the central Alaskan Beaufort Sea (Griffiths and Gallaway 1982; Critchlow 1983; Griffiths et al. 1983; Woodward-Clyde Consultants 1983; Moulton et al. 1986b). It is also one of the two primary species taken in a commercial fishery located in Alaska's Colville River delta (Fig. 1). The Colville River gillnet fishery has been in operation since 1967 and takes considerable numbers of arctic cisco during October and November of each year. The fishery is size selective and takes primarily 5- to 8-yr-old fish (Gallaway et al. 1983; Moulton et al. 1986a).

Because of their abundance in Alaskan waters, arctic cisco were thought to spawn in some of the larger river systems of the Alaskan North Slope. Recently, Gallaway et al. (1983) speculated that arctic cisco found in Alaskan waters may be spawned in Canada's Mackenzie River system (Fig. 1). Whereas there is virtually no evidence that arctic cisco spawn in Alaskan rivers, spawning migrations have been documented for numerous tributaries of the Mackenzie River system including the Peel, Arctic Red, Great Bear, Mountain, and Liard rivers (Hatfield et al. 1972; Stein et al. 1973; O'Neill et al. 1982; McLeod and O'Neill 1983).

Juvenile cisco hatched in the Mackenzie River system are transported downstream and reach the Mackenzie estuary in late spring. Gallaway et al. (1983) hypothesized that young-of-the-year fish are transported into Alaskan waters during the ice-free summer season by prevailing longshore currents. Once in Alaskan waters they take up residence in or near freshwater drainages of the North Slope. Here they remain until the onset of sexual maturity, at which point fish return to the Mackenzie River to spawn.

Subsequent evidence supports the hypothesis. Westward movement of age 0 arctic cisco along the Alaskan/Canadian Beaufort Sea coast was documented in 1985 (Fawcett et al. 1986; Cannon et al. 1987). In addition, Moulton et al. (1986a) observed that arctic cisco tagged as part of ongoing environmental monitoring programs disappear from Alaskan commercial fishery catches within 2 yr of having been marked. They

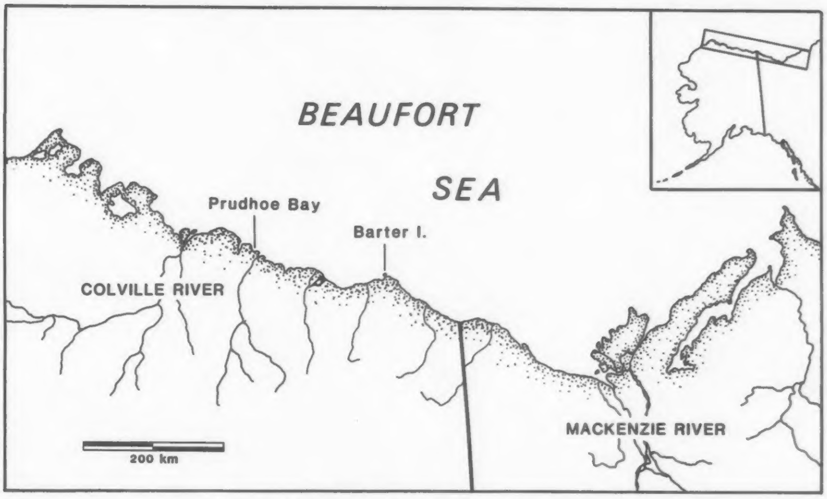


FIG. 1. Alaskan/Canadian Beaufort Sea coastline.

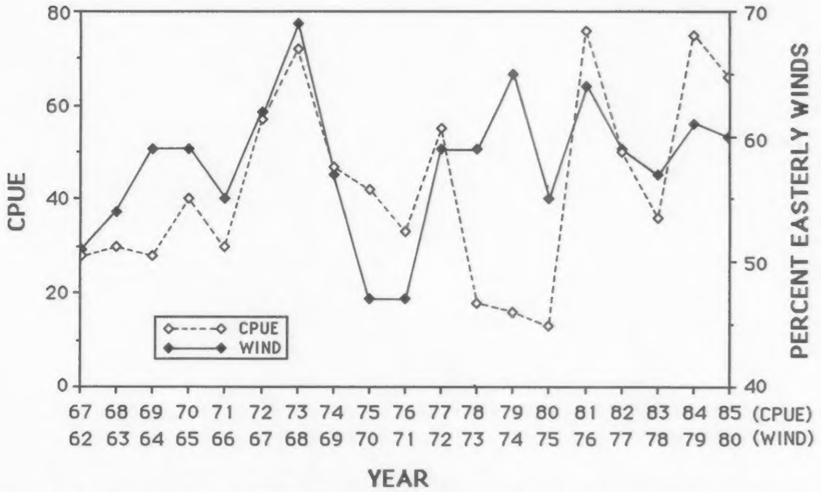


FIG. 2. Catch-per-unit-effort (CPUE) at Colville River commercial fishery and percent easterly winds during summer at Barter Island, by year.

pointed out that the rapid decline in tag returns would be consistent with the Mackenzie River origin hypothesis in that fish apparently leave local waters when they approach maturity.

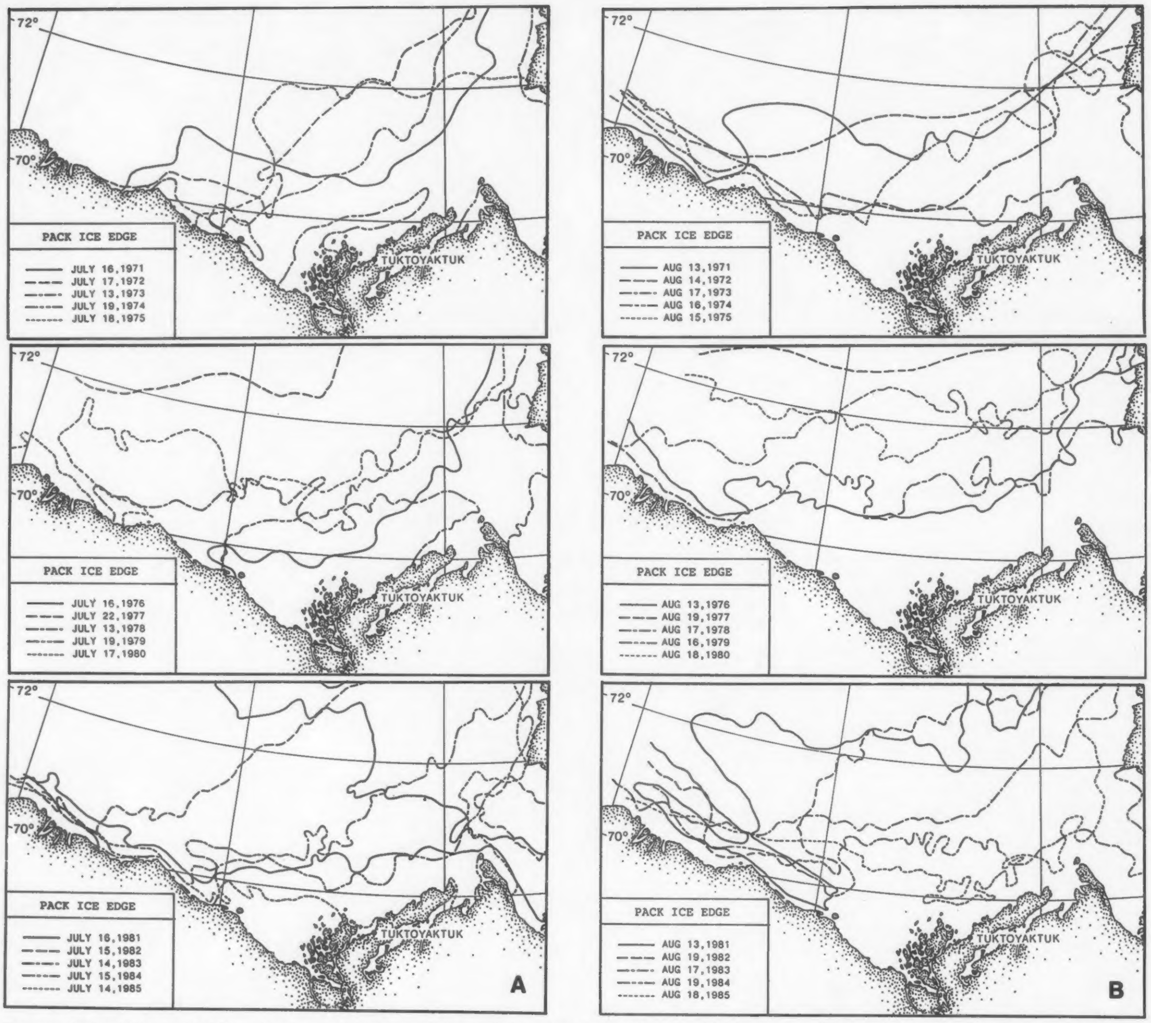
The purpose of this note is twofold. First, we offer further evidence in support of the Mackenzie River origin hypothesis. Second, we postulate that the magnitude of the annual harvest of arctic cisco in the Colville River commercial fishery may be linked to meteorological and oceanographic events that control the recruitment of young-of-the-year fish into Alaskan waters.

Methods

Assuming that the Mackenzie River origin hypothesis is correct, the recruitment of age 0 arctic cisco into Alaskan waters may depend, in part, upon longshore transport of juvenile fish along the Beaufort Sea coast. While deep, offshore currents flow from east to west as a result of the Arctic Basin Gyre, nearshore flow is primarily wind driven and therefore variable in direction (Aagaard 1978). Westward dispersal in the nearshore zone would be aided by a prevalence of easterly winds and inhibited by a prevalence of westerly winds.

To assess the effect of wind-driven currents on yearly recruitment, we compared summer wind patterns against commercial catches of arctic cisco at the commercial fishery. Wind data were recorded at a permanent weather station located at Barter Island, Alaska (Fig. 1). Wind was defined in terms of percent frequency of easterly winds during summer, i.e. the percent of time that winds blew from the eastern quadrant (45–135°) during June–September of each year (Hummer and Schrader 1984). Catch-per-unit-effort (CPUE) was defined as the number of fish caught per 50-m length of net per day.

Because arctic cisco are not recruited into the fishery (i.e. not large enough to be caught) until age 5+, CPUE would not be expected to reflect the magnitude of juvenile transport until 5 yr after dispersal from Canadian waters occurred. For ana-


72°
70°
PACK ICE EDGE
JULY 16,1971
JULY 17,1972
JULY 13,1973
JULY 19,1974
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AUG 13,1971
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JULY 16,1976
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JULY 14,1985
A
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B

FIG. 3. (A) Mid-July and (B) mid-August locations of the pack ice edge from 1971 to 1985 inclusive. The pack ice edge is taken as the contour line representing seven-tenths sea ice cover.

lytical purposes, the wind time series was shifted forward 5 yr to compensate for the 5-yr gap between arctic cisco recruitment into Alaskan waters and their recruitment into the fishery.

Results and Discussion

Wind patterns (as percent easterly winds) and commercial catch (as CPUE) were significantly related (Fig. 2; Spearman's rank correlation analysis, $p = 0.036$). Under meteorological conditions that promote westward transport (east winds), more arctic cisco appear to be recruited into Alaskan waters. This increased recruitment becomes manifest as an increase in commercial fishery catch some 5 yr later when fish have grown to a size that renders them susceptible to commercial gill nets. Results are consistent with the Mackenzie River origin hypothesis.

The most noticeable breakdown in the relationship occurred in 1978 and 1979. The data for these years should correspond to wind patterns in 1973 and 1974. This disparity between the two suggests that something in 1973 and 1974 may have disrupted normal recruitment of arctic cisco into Alaskan waters.

In the summer of 1974, unusually severe ice conditions prevailed in the eastern Beaufort Sea, with sea ice concentrations far in excess of those observed in any other year from 1971 to 1985 (Fig. 3). Heavy pack ice advanced into coastal regions during the spring of 1974, where it remained until September. Due to the severe ice conditions, outflow from the Mackenzie River was confined to areas immediately adjacent to the Mackenzie delta, rather than being dispersed over a much larger portion of the Beaufort Sea, as is the case in most summers (Marko 1975; Herlinveaux and de Lange Boom 1975).

The unusually severe ice conditions of 1974 would be expected to reduce recruitment of arctic cisco into Alaskan waters. Reduction could result from containment of age 0 fish within Mackenzie Bay due to direct blockage by sea ice. Lower recruitment rates could also result from reduced westward dispersal along the coastline because of limited overwater wind fetch.

The overwater fetch lengths for easterly winds were unusually low along the eastern Alaskan coastline during 1973–75 (Fig. 3). Over the 15-yr record from 1971 to 1985, these three years along with 1981 have the lowest easterly wind fetches during mid-July to mid-August. The low CPUE of 1978–80 may be partially related to the reduced summer wind fetches experienced 5 yr earlier in eastern Alaska.

Other sources of variability could also affect the magnitude of the commercial fishery catches. Fluctuations in the yearly reproductive success of Mackenzie River stocks would modify the number of young-of-the-year arctic cisco available for recruitment. The spatial effort expended by the commercial fishery is not always consistent between years because nets are sometimes moved to different locations within the Colville Delta in an attempt to maximize total catch. Because the commercial fishery takes 5- to 8-yr-old fish, strongly recruited cohorts can be expected to affect catch rates for several years. This multiple-year influence is partially offset by decreasing population size attributable to natural mortality. A native subsistence fishery based at the village of Nuiqsut on the Colville River competes directly with Helmericks commercial fishery and may account for 20–60% of all the arctic cisco taken locally (George and Nageak 1985; Moulton et al. 1986a). Gallaway et al. (1983) questioned whether the reestablishment of the village in 1973 may have contributed to lower commercial fishery CPUE during the following years (Fig. 2). Although the subsistence fishery may affect the yearly catch of arctic cisco in the commercial fishery, fluctuations in CPUE and percent easterly winds remained synchronous following 1973 with the exception of 1978 and 1979. These two years correspond to longshore recruitment into Alaskan waters in 1973 and 1974, two of the worst ice years during the period of record. Given these and other sources of variability, the robust association between wind and CPUE suggests that wind-driven currents may be a dominant mechanism in controlling the recruitment of arctic cisco.

This recruitment hypothesis has important implications regarding environmental impact assessments. In response to commercial development of petroleum reserves near Prudhoe Bay, Alaska (Fig. 1), extensive environmental monitoring surveys have been conducted in the region each year since 1981. Studies indicate that the Prudhoe Bay region is an important feeding and overwintering area for arctic cisco (Griffiths and Gallaway 1982; Critchlow 1983; Griffiths et al. 1983; Woodward-Clyde Consultants 1983; Biosonics Inc. 1984; Moulton et al. 1986b; Cannon et al. 1987). Although changes in commercial as well as the native subsistence harvest of arctic cisco could be construed as an indication of environmental impact caused by industry, such conclusions would be premature without first considering the potential effects of natural phenomena occurring some 5 yr earlier.

Recruitment projections based upon the wind-aided dispersal hypothesis could also be used as a baseline against which to measure environmental impact. Continued commercial development along the arctic coast would become suspect if it were accompanied by a decay in the relationship between prevailing wind patterns, ice cover, and the abundance of arctic cisco in Alaskan waters.

The recruitment of arctic cisco into Alaskan waters also has implications regarding the stability of Canadian populations. Although arctic cisco are known to inhabit waters along the Canadian coast (Kendel et al. 1975; Percy 1975; Bond 1982; Lawrence et al. 1984), there are no data to indicate the proportion of newly emerged fish that disperse westward to Alaska under specific meteorological regimes. If this proportion is large, then the integrity of Mackenzie River stocks could be strongly dependent upon the success of the Alaskan migrants. The role of active migration on yearly recruitment also needs to be investigated.

Acknowledgments

We thank Benny Gallaway, William Griffiths, David Schmidt, and Joe Truett for critically reviewing the manuscript and Environment Canada (Atmospheric Environment Service) for providing data from which sea ice charts were derived.

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Comparison of in situ Estimates of Chlorophyll *a* Obtained with Whatman GF/F and GF/C Glass-Fiber Filters in Mesotrophic to Hypereutrophic Lakes[1]

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Prepas, E. E., M. E. Dunnigan, and A. M. Trimbee. 1988. Comparison of in situ estimates of chlorophyll a obtained with Whatman GF/F and GF/C glass-fiber filters in mesotrophic to hypereutrophic lakes. Can. J. Fish. Aquat. Sci. 45: 910–914.

In response to the recent attention given to picoplankton, many researchers have switched from GF/C to GF/F glass-fiber filters for chlorophyll a (Chl a) analyses; GF/F filters have a smaller pore size and are more expensive than GF/C filters. In this study, Chl a was measured with both Whatman GF/F and GF/C glass-fiber filters on euphotic zone water from 28 mesotrophic to hypereutrophic lakes (Chl a ranged from 2 to 175 $\mu g \cdot L^{-1}$) in central Alberta. The differences between paired Chl a estimates with the two grades of filter paper were remarkably small; there was no evidence that GF/F filters collected more Chl a than GF/C filters ($P > 0.2$). Hence there is no justification for switching from GF/C to GF/F filters for routine Chl a analyses on productive lakes.

Par suite de l'attention récente portée au picoplancton, de nombreux chercheurs ont commencé à utiliser des filtres de fibre de verre GF/F au lieu de filtres GF/C pour les analyses de chlorophylle (Chl a) les filtres GF/F ont des pores de moins grande dimension et coûtent plus cher que les filtres GF/C. Dans cette étude, la Chl a a été mesurée avec des filtres de fibre de verre Whatman GF/F et GF/C dans de l'eau de la zone euphotique provenant de 28 lacs mésotrophes à hypereutrophes du centre de l'Alberta (les mesures de la Chl a variaient entre 2 et 175 $\mu g \cdot L^{-1}$. Les différences entre les estimations de la Chl a obtenues avec les deux qualités de papier filtre étaient remarquablement faibles; rien ne permettait de conclure que les filtres GF/F recueillaient plus de Chl a que les filtres GF/C ($P > 0,2$). Par conséquent, il n'y a aucune raison de substituer des filtres GF/F aux filtres GF/C pour les analyses courantes de la Chl a dans les lacs productifs.

Received September 28, 1987
Accepted January 15, 1988
(J9437)

Reçu le 28 septembre 1987
Accepté le 15 janvier 1988

Picoplankton, phytoautotrophic microorganisms which range in size from 0.2 to 2.0 μm, can be a significant portion of the algal biomass in lakes (up to 37% of total biomass in four studies and 70% of total primary production in six studies) (Stockner and Antia 1986; Caron et al. 1985). Most studies on picoplankton have been on oligotrophic systems (Stockner and Antia 1986). It has been suggested that picoplankton make a larger contribution to biomass and production in oligotrophic than in more eutrophic systems (Lee and Nalewajko 1978; Stockner and Antia 1986), although this concept has not been evaluated quantitatively.

Chlorophyll *a* (Chl *a*) is routinely used as an estimate of algal biomass in aquatic studies (Vollenweider 1969). Chl *a* has often been measured with Whatman GF/C glass-fiber filters (Schindler et al. 1971; Dillon and Rigler 1974; Stainton et al. 1977; Prepas and Trew 1983), which have a nominal pore size of 1.2 μm and a median retention size of 0.7 μm (Sheldon 1972). With the recent attention given to picoplankton (Johnson and Sieburth 1979; Waterbury et al. 1979), researchers have switched to the more expensive Whatman GF/F glass-fiber filters (e.g. Burnison 1980; Li et al. 1983; Smith et al. 1985; Murphy et al. 1985; Stockner and Shortreed 1985; Stockner and Antia 1986) for Chl *a* analyses. GF/F filters have a smaller nominal pore (0.7 μm) and median retention size (~0.2 μm) than GF/C filters. However, we are unaware of an evaluation of whether this switch to a more expensive filter paper (approximately twice the cost) has an effect on in situ estimates of Chl *a*.

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[1] This project was based at the Meanook Biological Research Station.

In the summer of 1986 we collected data on euphotic zone Chl *a* (with both Whatman GF/F and GF/C filters) and biogeochemical parameters from 28 lakes in central Alberta. These data were used to evaluate the relative efficiencies of the two grades of glass-fiber filter for Chl *a* estimates in mesotrophic to hypereutrophic lakes.

Materials and Methods

From May through August 1986, 28 lakes in central Alberta were sampled three times for biogeochemical parameters. From 21 July through 18 August 1986, samples for Chl *a* analyses were filtered through both Whatman GF/C and GF/F filters.

Vertical profiles of temperature and light were measured at the deepest site in the lake on each visit. Temperature (degrees Celsius) was measured at 0.25- to 1-m intervals with a Hydrolab model TDO-2 resistance thermometer accurate to 0.25°. The bottom of the trophogenic zone was defined as the depth where 1% of surface light penetrated, as measured with a Protomatic photometer (Protomatic, Dexter MI). True duplicate samples for all analyses were collected from the trophogenic zone with weighted Tygon tubing. A trophogenic sample consisted of water pooled from three to five sites in the lake; the number of sites sampled was proportional to the lake surface area. At no time was the Tygon tubing allowed to go deeper than 0.25 m above the bottom.

Samples for total Kjeldahl nitrogen (TKN) analyses were placed in 250-mL polystyrene containers and acidified within 1 h of collection with 1 mL of 10 N sulfuric acid. Samples for total phosphorus (TP), conductivity, $NO_2 + NO_3$, pH, colour, turbidity, and Chl *a* analyses were placed in Nalgene polyethylene bottles (opaque bottles were used for Chl *a*). All bottles were completely filled with lake water and stored on ice in coolers and then refrigerated at 4°C until the water was analyzed. The containers for nitrogen analyses were cleaned with double-distilled water (DDW) only; all other containers were acid washed in 2% HCl and rinsed with DDW. Within 12 h of collection, water samples for TP analyses were prefiltered through a 250-μm Nitex net and transferred to culture tubes (after Prepas and Rigler 1982). Samples for Chl *a* analyses were filtered (volume filtered 50–400 mL, median value 200 mL) under low pressure (maximum −50 kPa) through Whatman GF/C or GF/F glass-fiber filters. These filters were placed in petri dishes, wrapped in aluminum foil, and frozen.

Sample pH was measured with a Beckman Expandomatic SS-2 meter. Conductivity was measured with a YSI model 31 conductivity bridge on water samples at 20°C. Colour was measured visually after samples were centrifuged for 10 min on a Hazen platinum–cobalt scale with a Hellige-Aqua tester (model 611-A). Turbidity was measured with a Hach turbidimeter (model 2100 A). TKN was analyzed by Solorzano's (1969) phenolhypochlorite method as modified by Prepas and Trew (1983). $NO_2 + NO_3$-N was determined after filtration through a prewashed 0.45-μm HAWP Millipore membrane filter by the automated cadmium–copper reduction method (Stainton et al. 1977). Total nitrogen (TN) was calculated as the sum of TKN and $NO_2 + NO_3$. TP was analyzed by Menzel and Corwin's (1965) potassium persulfate method. All analyses for nitrogen and TP were done in triplicate. Chl *a* was determined in duplicate with a spectrophotometric technique based on the ethanol extraction procedure of M. Ostrofsky (Biology Department, Alleghany College, Meadville, PA, unpubl.) described by Bergmann and Peters (1980). The ethanol extraction method gives values that are not statistically different from Yentsch and Menzel's (1963) acetone extraction technique, which corrects for phaeophytin (Prepas 1984). Samples for nitrogen were analyzed within 48 h of collection, for Chl *a* within 2 wk, and all other analyses within 7 d.

All analyses were performed separately on the true duplicated samples collected from the trophogenic zone of each lake. Thus the values reported here are based on an average of four (i.e. Chl *a*) or six (e.g. TP, nitrogen) separate determinations. For all analyses except Chl *a*, the data were averaged over the study period (number of collections = 3) and are referred to as average summer.

Statistical analyses follow Snedecor and Cochran (1980).

Description of the study lakes — The study lakes are located in central Alberta, within 100 km of the Meanook Biological Research Station (Table 1). They are situated in the mixed-wood region of the boreal forest (Strong and Leggat 1981), and the drainage basins cover the spectrum from completely forested to mostly cleared for grazing and cereal crops. The climate is continental; mean annual precipitation and lake evaporation are 400–500 and 500–600 mm, respectively (Fisheries and Environment Canada 1978). The lakes are situated in glacial till underlain by sedimentary bedrock.

The lakes are representative of small to medium-sized water bodies in central Alberta. They range from tiny to moderate sized (surface areas from <0.01–8 km²) and maximum depth varies from 2 to 35 m. Although four of the water bodies are small enough to be referred to as ponds or dugouts, the term lake will be used for all 28. Most of the lakes (i.e. 21) were thermally stratified during the study period; seven were usually isothermal. All but one of the lakes contained fresh water; Auger Lake was mildly saline (Rawson 1951). The summer pH in the study lakes was high (7.2–9.3). Colour was low (<30 mg $Pt \cdot L^{-1}$) in all but seven of the lakes; the coloured lakes were small (colour ranged up to a maximum average summer value of 143 mg $Pt \cdot L^{-1}$). The lakes were not turbid (≤ 18 JTU) and all are well buffered (Table 1).

The study lakes varied from mesotrophic to hypereutrophic (Wetzel 1985). Average summer TN and TP ranged from 534 to 3028 and from 10 to 177 $\mu g \cdot L^{-1}$, respectively (Table 1). Average summer $NO_2 + NO_3$ varied from 4 to 56 $\mu g \cdot L^{-1}$ (data not shown). The TN to TP ratios varied from 4 to 90: in over half the lakes (i.e. 16) the ratios were greater than 30, and in only one lake (Canoe Lake) it was less than 14 (Table 1). These lakes are phosphorus limited during most of the summer (Prepas and Trew 1983; Prepas 1983; Prepas and Trimbee 1987).

TABLE 1. Location, thermal regime (S, stratified; I, isothermal), surface area (area), maximum dept
(total phosphorus (TP) concentration, TN to TP ratios (TN:TP)), and chlorophyll *a* (Chl *a*) conc
grade was varied (i.e. Whatman GF/F or GF/C glass-fiber filters) for the 28 study lakes. All che
trophogenic zone in 1986. The Chl *a* analyses are from one sampling date from mid-July through

Lake	Lat. (°N)[b]	Long. (°W)[b]		Area (km²)	Z (m)	Conductivity (μS·cm⁻¹)	pH	Colour (mg Pt·L⁻¹)	Turbidit (JTU)
Antoine	54°46′	112°05′	S	3.58	7.6	436	8.8	12	18
Auger	54°43′	112°31′	I	1.85	2.0	697	9.1	23	3
Canoe	54°37′	113°08′	I	1.03	2.6	357	9.3	37	4.3
Crooked[a]	54°55′	113°33′	S	2.38	9.5	281	8.6	20	5
East Meanook Pond[a]	54°37′	113°21′	S	0.002	3.9	168	7.7	143	2
Ghost	54°53′	113°37′	S	1.98	14	285	8.7	15	2
God's	54°23′	113°38′	I	2.21	4.6	279	8.3	9	2
Halfmoon	54°04′	113°21′	I	0.79	6.6	397	8.4	15	1
Hanmore	54°17′	112°31′	S	2.86	25	331	8.7	7	2
Hope	54°39′	112°41′	S	2.73	16	279	8.7	2	1
Island (N.)	54°50′	113°31′	S	7.78	21	—	—	—	—
Jackfish	54°48′	113°05′	I	2.17	5.8	228	8.3	6	1
Jenkins[a]	54°46′	113°36′	S	1.62	17	244	8.9	16	5
Lodge	54°43′	112°26′	S	2.41	23	268	8.5	3	1
Lofty[a]	54°43′	112°29′	S	0.70	7.0	303	8.8	29	11
Long	54°35′	113°39′	S	1.62	28	312	7.9	15	1
Long Island	54°27′	113°47′	S	1.89	15	235	8.2	11	1
Lower Chain	54°58′	113°30′	S	0.84	9.5	378	8.5	9	1
Middle Chain	54°58′	113°30′	S	0.89	10	500	8.4	10	1
Mons	54°11′	112°22′	I	2.77	7.0	476	8.5	9	2
Narrow	54°35′	113°37′	S	1.14	35	290	8.2	10	1
Peter's Dugout	54°34′	113°33′	S	0.001	6.8	215	7.8	67	1
Tawatinaw	54°20′	113°28′	S	0.48	4.3	321	7.8	60	1
Unnamed (South Baptiste)	54°41′	113°36′	S	0.9	8.9	315	8.0	27	2
Unnamed (Teen)	54°29′	113°43′	S	0.32	8.6	293	8.2	21	1
Unnamed (Tonn)	54°38′	113°35′	S	0.03	5.2	1247	7.9	104	4
Westlock Dugout	54°09′	113°43′	I	0.002	4.9	343	8.5	37	6
West Meanook Pond[a]	54°37′	113°21′	S	0.001	2.7	1143	7.2	105	12

[a] *Aphanizomenon flos-aquae* flakes > 5 mm in length present in the sample.

[b] Locations for unnamed lakes, ponds, and dugouts were obtained from 1:50,000 topographic map
(1958).

um depth (*Z*), pH, colour, turbidity, conductivity, nutrients *a*) concentrations for duplicate analyses where only filter All chemical data, except for Chl *a*, are averages for the through mid-August.

Turbidity (JTU)	TP (μg·L^{-1})	TN:TP	Chl *a* (μg·L^{-1})		
			GF/C	GF/F	GF/C:GF/F
18	177	14	88.2	82.2	1.07
	—	—	63.9	68.2	0.94
3	72.7	41	9.2	9.0	1.02
	—	—	27.1	25.2	1.08
4.3	440	4.1	70.0	69.9	1.0
5	47.9	30	75.6	78.0	0.97
2	132	20	10.8	11.1	0.97
2	50.0	24	15.0	14.9	1.01
2	39.6	34	12.9	12.9	1.0
1	38.9	31	14.8	14.2	1.04
2	17.0	40	5.5	4.9	1.12
1	18.0	48	4.8	4.9	0.98
—	20.4	56	6.0	6.4	0.94
1	19.4	52	3.8	3.7	1.03
5	39.6	32	39.9	40.3	0.99
1	16.8	48	4.5	4.3	1.05
11	135	22	100.5	96.8	1.04
	—	—	175.1	171.5	1.02
1	13.2	50	3.4	3.3	1.03
1	21.7	42	5.0	5.0	1.0
1	12.8	85	2.9	3.0	0.97
1	16.1	89	3.4	3.3	1.03
2	35.5	32	6.5	6.8	0.96
1	10.5	51	3.3	3.2	1.03
1	43.1	25	1.9	1.8	1.06
1	77.4	17	5.4	5.4	1.0
2	33.9	27	16.4	15.0	1.09
1	24.2	40	7.0	6.7	1.05
4	55.6	28	22.4	23.1	0.97
6	54.0	23	10.0	9.5	1.05
12	44	15	32.0	30.5	1.05

hic maps; all others were from Gazeteer of Canada, Alberta

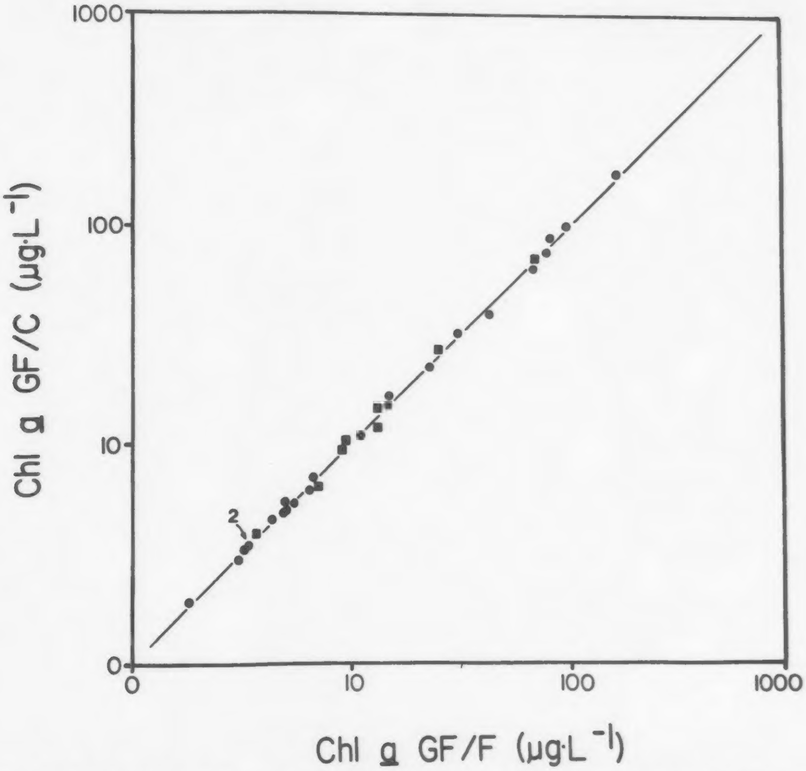

FIG. 1. Chlorophyll *a* (Chl *a*) concentrations measured on Whatman GF/F and GF/C filters in 28 (three lakes were sampled twice for this comparison) mesotrophic to hypereutrophic lakes in Alberta. The lakes are divided into two mixing regimes: thermally stratified (●) and isothermal (■). The line is 1:1.

Results and Discussion

During midsummer when Chl *a* was analyzed on both Whatman GF/F and GF/C filters, Chl *a* ranged from 2 to 175 $\mu g \cdot L^{-1}$ in the study lakes (Table 1). The differences between Chl *a* collected on the two grades of filter paper were remarkably small; the average difference was less than 1 $\mu g \cdot L^{-1}$ for analyses which averaged 27 $\mu g \cdot L^{-1}$ (Table 1). There was no evidence in our data set that GF/F filters retained consistently more Chl *a* than GF/C filters (Fig. 1; paired *t*-test, $P > 0.2$). In addition, the average variance for replicate Chl *a* samples analyzed on GF/F and GF/C filter paper were remarkably similar ($\bar{s}^2 = 2.14$ and 2.16 $\mu g \cdot L^{-1}$, respectively).

The lakes were separated into thermally stratified and usually isothermal, based on a suggestion that picoplankton may be less important under mixed conditions (Nalewajko and Voltolina 1986). However, there were no differences in Chl *a* retained on the two sizes of filter in both lake types (Fig. 1). We also looked at whether there was a relationship between ($\log_{10}$) average summer TP concentration (as an index of trophic status) and the differences in Chl *a* collected on the two grades of glass-fiber filter; there was no pattern ($r^2 = 0.06$, $P > 0.5$). Differences (both positive and negative) in Chl *a* on the two filter types were greatest when TP (and Chl *a*) concentrations were highest (Table 1). This increased variation with increased productivity is likely due to the higher sampling variation encountered when larger algal forms (e.g. *Aphanizomenon flos-aquae* flakes) were present, as is common in the more productive systems.

The differences between Chl *a* retained on Whatman GF/F and GF/C glass-fiber filters in these mesotrophic to hypereutrophic lakes were insignificant. These results are not likely related to our processing technique, as samples were filtered at low vacuum to avoid cell rupture (Li et al. 1983; Smith et al. 1985). All Chl *a* concentrations in Table 1 are the average of four separate determinations. Our results are independent of colour, turbidity, and TN to TP ratios (Table 1) and span a broad range in productivity (2–175 μg Chl $a \cdot L^{-1}$).

There are at least two plausible explanations for the results obtained in our study: (1) the small difference in pore and retention sizes of the two grades of filter (~0.5 μm) was too small to expect significant differences, given the variable retention capabilities of these filters (Sheldon 1972) and (2) picoplankton are a relatively small proportion of overall algal biomass in (at least some) mesotrophic to hypereutrophic lakes in midsummer. Thus, we found no consistent differences in Chl *a* on filters with median retention sizes of ~0.2 and 0.7 μm because picoplankton in this size range are relatively unimportant in eutrophic lakes.

We concluded that (1) Whatman GF/C glass-fiber filters are adequate for routine estimates of Chl *a* in mesotrophic to hypereutrophic lakes and (2) the relative importance of picoplankton should be quantified in a range of mesotrophic to hypereutrophic lakes. We see no justification for switching to the (~100%) more expensive GF/F glass-fiber filters for Chl *a* analyses in productive lakes. In our laboratory the difference in cost would be ~$800.00 per year if we switched to GF/F filters.

Acknowledgements

We thank C. Wiebe, G. Hutchinson, D. Webb, L. Parker, N. C. Robinson, and K. Gibson for their assistance with field collections and laboratory analyses, J. M. Hanson, P. Chambers, M. Stainton, and J. G. Stockner for helpful comments on the manuscript, D. O. Trew for his support of this study, and the Natural Sciences and Engineering Research Council of Canada and the Water Quality Control Branch of Alberta Environment for financial support in the form of an operating grant and contract, respectively, to E.E.P. A.M.T. was supported with a grant from the Alberta Environmental Research Trust.

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Contrasting Patterns of Net- and Nanoplankton Production and Biomass among Lakes

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Watson, S., and E. McCauley. 1988. Contrasting patterns of net- and nanoplankton production and biomass among lakes. Can. J. Fish. Aquat. Sci. 45: 915–920.

The relative contribution of nanoplankton to total algal biomass was shown to be negatively correlated with total phosphorus during summer over a wide range of lakes. We hypothesize that this pattern can be explained either by changes in the relative growth rates of net- or nanoplankton with increased nutrient levels, or through the regulation of the nanoplankton biomass by herbivores, allowing disproportionate increases in netplankton biomass in more eutrophic systems. These explanations were tested by examining the relationships between net primary production (grams of carbon per cubic metre per year) and biomass (micrograms per litre) of these size fractions and total phosphorus concentrations (micrograms per litre) using literature data from lakes throughout the world. The production of the net- and nanoplankton vary similarly with total phosphorus, while the biomasses (and thus the ratios of production to biomass) of the two groups show significantly different relationships. Our results support the hypothesis that changes in the size distribution of summer phytoplankton with enrichment seem to be influenced more by herbivores than by changes in the relative growth rates of the two size fractions.

On montre que la contribution relative du nannoplancton à la biomasse algale totale est en corrélation négative avec la teneur totale en phosphore pendant l'été dans une grande variété de lacs. On formule l'hypothèse que cette relation peut être expliquée soit par des variations des taux relatifs de croissance du nannoplancton ou du microplancton liées à des teneurs élevées en bioéléments ou par le contrôle de la biomasse nannoplanctonique par les herbivores; ces alternatives mènent à des augmentations inégales de la biomasse microplanctonique dans les systèmes plus eutrophes. On se sert des relations entre, d'une part, la production primaire nette (grammes de carbone par mètre cube par an) et, d'autre part, la biomasse (microgrammes par litre) de ces composantes et les teneurs totales en phosphore (microgrammes par litre), (relations élaborées à partir de données publiées sur des lacs du globe. La production de nannoplancton et de microplancton varie de façon semblable en fonction de la teneur totale en phosphore tandis que les biomasses (et donc les rapports entre la production et la biomasse) des deux composantes montrent des relations nettement différentes. Les résultats obtenus étayent l'hypothèse que les herbivores influent plus sur les variations de la distribution de tailles chez le phytoplancton estival résultant de l'enrichissement que les variations des taux relatifs de croissance des deux composantes.

Received May 12, 1987
Accepted January 25, 1988
(J9282)

Reçu le 12 mai 1987
Accepté le 25 janvier 1988

Many studies have shown that total algal biomass increases with eutrophication (e.g. Kalff and Knoechel 1978; Nicholls and Dillon 1978; Schindler 1978), but few simple relationships between algal community structure and nutrients have been identified. This may reflect both the difficulty of estimating the structure and biomass of the highly complex phytoplankton assemblages present in lakes and the diversity of approaches that have been taken to describe community structure. While some authors prefer taxonomic descriptions (e.g. Ahlgren 1970; Nicholls 1985; Reynolds 1984; Willén 1980), others examine the distribution of biomass among various size categories (e.g. Pavoni 1963; Kalff 1972; Spodniewska 1978, 1983; Sprules and Munawar 1986; Bailey-Watts 1986). The problem is compounded further because taxonomic composition and size structure may co-vary among natural systems. In this note, we examine variation in size structure with increasing eutrophication and use the considerable literature on size-dependent processes to advance explanations for the relationships we present. We concentrate on periods of summer stratification to reduce the impact of large-scale environmental variability associated with spring and fall overturn.

Phytoplankton communities have been divided into numerous overlapping and often quite arbitrary size categories, and several authors have stated the need for a standard system of classification and nomenclature (Gelin and Ripl 1978; Rai 1982; Sicko-Goad and Stoermer 1984; Stockner and Antia 1986). Recent reviews have proposed a series of divisions, ranging from very small (<2–3 μm; picoplankton) to larger size categories (e.g. Sieburth et al. 1978; Stockner and Antia 1986). However, for the purposes of the study, we take a simplified functional approach and consider only two major groups based on their availability to herbivorous zooplankton: nanoplankton or "edible" algae and netplankton or "inedible" algae. Since zooplankton readily ingest particles up to approximately 35 μm (e.g. Gliwicz 1977), we have extended the nanoplankton, previously defined as <20 μm (Sieburth et al. 1978), to include phytoplankton with an upper size limit of approximately 35 μm.

Over the entire growing season, including spring, summer, and fall periods, the proportion of nanoplankton biomass (micrograms per litre) decreases with increased total algal biomass for a wide range of lakes (Watson and Kalff 1981; Kalff and Watson 1986). We first determine whether this relationship is simply an artifact of combining spring, summer, and fall data by using observations taken only from periods of relative environmental stability (generally, mean summer values).

If we assume that the observed variation in phytoplankton community size structure with enrichment is produced by interactions among the various algal species and other biotic components of their environment, then we can advance two extreme or opposing hypotheses. (1) The observed variation in the proportion of net- and nanoplankton is produced by changes in their relative growth rates with increased nutrient supply. Netplankton appear to increase their competitive advantage with increasing total algal biomass. This hypothesis stresses changes in the outcome of competition among algal species based on relative changes in size-specific growth rates in response to enrichment. (2) The proportion of netplankton increases not because of a change in their competitive ability, but because the nanoplankton (edible algae) are regulated by herbivores. Therefore, enrichment simply increases the biomass of netplankton (inedible algae) and results in a concomitant increase in the average biomass of herbivorous zooplankton. This hypothesis does not necessarily require changes in relative growth rates of small and large phytoplankton with enrichment.

Obviously, these two explanations are not mutually exclusive, but in the extreme they make very different predictions about variation in size-specific phytoplankton production rates and changes in herbivore biomass with eutrophication.

Unfortunately, growth rates are extremely difficult to measure in situ, and there are only a few estimates for individual species from a narrow range of natural systems (Knoechel and Kalff 1978; Paerl and Mackenzie 1977). However, specific growth rates are significantly related to net primary production (Peterson 1978, 1980), and while there are pitfalls in interpreting production estimates (e.g. Peterson 1980; Stockner and Antia 1986), these problems should not bias results of broad-scale comparisons.

Phosphorus is generally the primary factor limiting phytoplankton growth and production in most lakes (e.g. Schindler 1978), and we consider total phosphorus (TP; micrograms per litre) as a measure of enrichment (e.g. Dillon and Rigler 1974; Kalff and Knoechel 1978; Nicholls and Dillon 1978; Smith 1979, 1982, 1986). Previous studies have mixed data from spring, summer, and fall and have reported different relationships between mean seasonal TP and nanoplankton biomass (e.g. Watson and Kalff 1981; Paloheimo and Zimmerman 1983). In this note, we examine how the average summer biomass (micrograms per litre) of net- and nanoplankton varies with mean summer TP among lakes of varying trophic state, and we compare these relationships with corresponding relationships between summer TP and net annual primary production (grams of carbon per cubic metre per year) for the same algal fractions.

Materials and Methods

The relationship between nanoplankton (edible) and total algal biomass was reanalyzed using summer mean values from the period between the spring and fall algal peaks for temperate lakes; data from tropical lakes (Oloidien and Naiwasha) (Kalff and Watson 1986) excluded observations from the wet season. Our dataset[1] included values for one or more years from 28 lakes, and combined data from most of the lakes examined by Watson and Kalff (1981) with observations from more recent publications, using only citations reporting algal biomass as wet weight. Where necessary, units were standardized to micrograms per litre from areal or volumetric estimates. While the definition of nanoplankton varied among authors, most used an upper size limit of 20–40 μm to delineate this fraction, and multivariate analysis showed that these differences in size limits did not significantly bias the results ($P > 0.05$; df = 70).

To test our initial hypotheses, we examined two groups of relationships. The first of these was between TP (micrograms per litre) and edible and inedible algal biomass (micrograms wet weight per litre) (Dataset I). These relationships were tested using (1) mean summer values from a range of lakes and studies and (2) a series of individual measurements taken on single sampling dates within the summer period from each of 55 Polish lakes, ranging in nutrient status (Spodniewska 1978, 1983).

The second set of relationships examined was between TP and edible and inedible net primary production averaged over the euphotic zone (grams of carbon per cubic metre per year) (Dataset II).

Regression relationships were determined using ordinary least-squares, and statistical differences among slopes were examined using appropriate t-tests with $\alpha = 0.05$.

Unfortunately, there are few studies in which all variables of interest were measured concomitantly. Thus, tests of predictions assume that the sample regression functions provide unbiased estimates of the population regression function (Gujarati 1978). In addition, since there is error associated with both the independent and dependent variables, Model II regression analysis would be more appropriate for our dataset, but there are insufficient data to use methods that allow confidence intervals of slopes and intercepts to be calculated (e.g. Bartlett's three-group method). Therefore, we used Model I analyses and confirmed each trend by calculating and comparing the geometric regression coefficients (e.g. Prepas 1984).

Results and Discussion

The relationship between mean summer nanoplankton (edible) and total algal biomass is highly significant (Fig. 1):

$$\log_{10} \text{edible biomass} = 0.727 + 0.617 \log_{10} \text{total biomass}$$
$$(n = 73; r = 0.86; P < 0.0001).$$

Since the slope is significantly less than 1 (t-test; $P < 0.05$), we can conclude that the size structure of summer algal communities does indeed change such that the relative proportion of the edible fraction decreases with enrichment. Furthermore, the slope of our regression using summer mean values is not significantly different from that obtained by Watson and Kalff

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[1] A complete set of tabular data is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2.

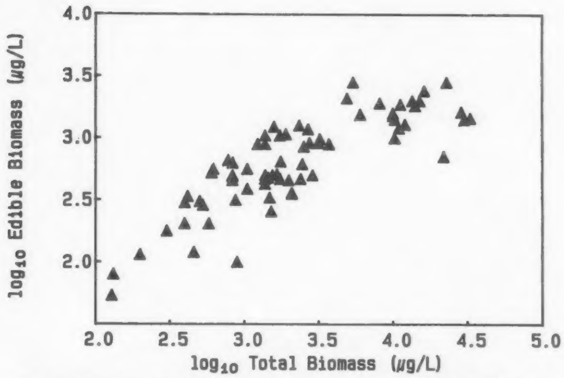

FIG. 1. Relationship between mean summer total and edible algal biomass:

$$\log_{10} \text{edible biomass} = 0.727 + 0.617 \log_{10} \text{total biomass} \quad (n = 73;\ r = 0.86,\ P < 0.0001).$$

Observations from the following lakes: Bavelse (Kristiansen 1971), Castle (Redfield 1982), Cayuga (Godfrey 1982), Como (Ruggiu 1983), Constance (Tilzer et al. 1985), Erie (Munawar and Munawar 1981), Esrom (Kristiansen 1971), Hall (Taylor 1981), Hanna (Sheath et al. 1975a), Hertel (Kalff 1972), Huron (Munawar and Munawar 1981), Kinneret (Pollingher 1986), Langvatn (Reinertsen and Langeland 1982), Leman (Balvay et al. 1984), LEWG M8 and N4 (Gates et al. 1983), Maarsseveen (Dorgelo et al. 1981; Koning and Dorgelo 1982), Memphremagog (Watson 1979), Maggiore (Ruggiu 1983), Mikolajskie (Hillbricht-Ilkowska et al. 1979), Mirror (Likens 1985), Naiwasha (Kalff and Watson 1986), Nora (Sheath et al. 1975a, 1975b; Sheath and Helleburst 1978), Oloidien (Kalff and Watson 1986), Pääjärvi (Granberg 1970), Superior (Munawar and Munawar 1981), Tystrup (Kristiansen 1971), and Washington (Edmondson and Litt 1982).

(1981) who used both spring and summer values, indicating that this pattern is independent of large environmental changes associated with spring and fall periods.

Algal community structure in relation to total phosphorus — Our results show that mean summer edible biomass is not strongly dependent on TP among a broad collection of lakes (Fig. 2A), as indicated by the small slope of the relationship. Based on regression analysis (Table 1), an order of magnitude increase in mean summer TP produces only an approximately twofold increase in the biomass of the edible fraction. In contrast, the inedible biomass shows more than a 20-fold increase over the same range of TP (Fig. 2B; Table 1). The slopes of these two relationships are significantly different ($P < 0.05$). Similar results can be obtained using individual data rather than mean values. The equations generated using these data had slopes and intercepts that were indistinguishable statistically from those we obtained using summer means (Table 1). Thus, the pattern of change in phytoplankton community size structure we observed using total algal biomass as an indicator of enrichment (Fig. 1) is exhibited again here using TP. This is significant, not only because TP is a more direct measure of enrichment, but also because the use of this variable in our analysis removes the problem of autocorrelation which was inherent in the earlier models.

A comparison of these summer relationships with regressions based on data from the entire growing season (e.g. Watson and Kalff 1981) shows two things. First, while the relationships between TP and inedible biomass from the two different seasons are virtually identical, there is a significant difference between the slopes of the two corresponding edible biomass equations ($P < 0.001$; Table 1; Watson and Kalff

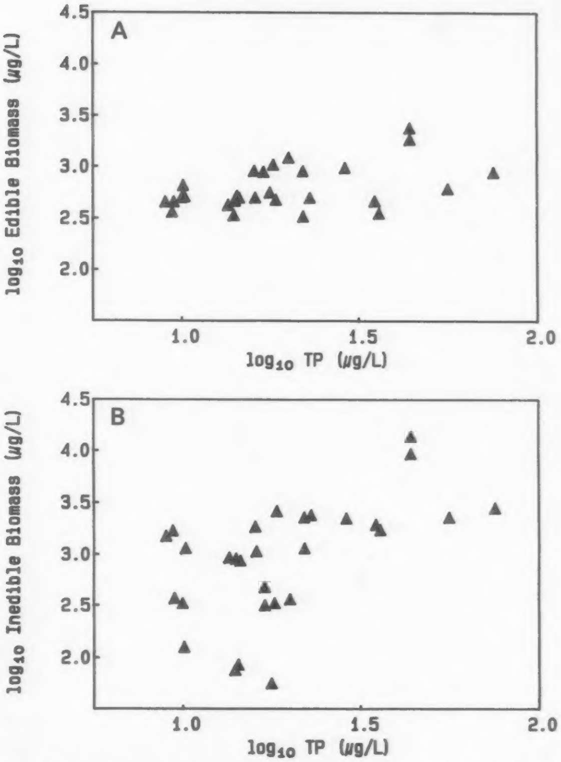

FIG. 2. Relationship between mean summer TP and (A) edible and (B) inedible phytoplankton biomass. Data were taken from one or more years from the following lakes (sources as in Fig. 1): Como, Constance, Hall, Hertel, Kinneret, Langvatn, LEWG M8 and N4, Memphremagog, Mikolajskie, Naiwasha, Nora, and Oloidien.

TABLE 1. Regression analysis. eB = edible biomass (µg/L); iB = inedible biomass (µg/L); ePP = edible primary production (g $C \cdot m^{-3} \cdot yr^{-1}$); iPP = inedible primary production (g $C \cdot m^{-3} \cdot yr^{-1}$); TP = total phosphorus (µg/L); SM = summer mean values; IP = individual points from the summer period.

Equation	R	df	P	Data type
Dataset I				
(1) log (eB) = 2.28 + 0.41 log (TP)	0.46	27	0.0029	SM
(1a) log (eB) = 2.20 + 0.57 log (TP)	0.43	53	0.0005	IP
(2) log (iB) = 1.27 + 1.32 log (TP)	0.56	27	0.0002	SM
(2a) log (iB) = 1.29 + 1.17 log (TP)	0.55	53	0.0005	IP
(3) log (iB) = 1.67 + 0.37 log (eB)	0.72	69	0.0000	SM
(3a) log (iB) = 2.21 + 0.31 log (eB)	0.50	53	0.0005	IP
Dataset II				
(4) log (ePP) = −0.37 + 1.14 log (TP)	0.95	21	0.0001	SM
(5) log (iPP) = −0.88 + 1.26 log (TP)	0.82	21	0.0001	SM

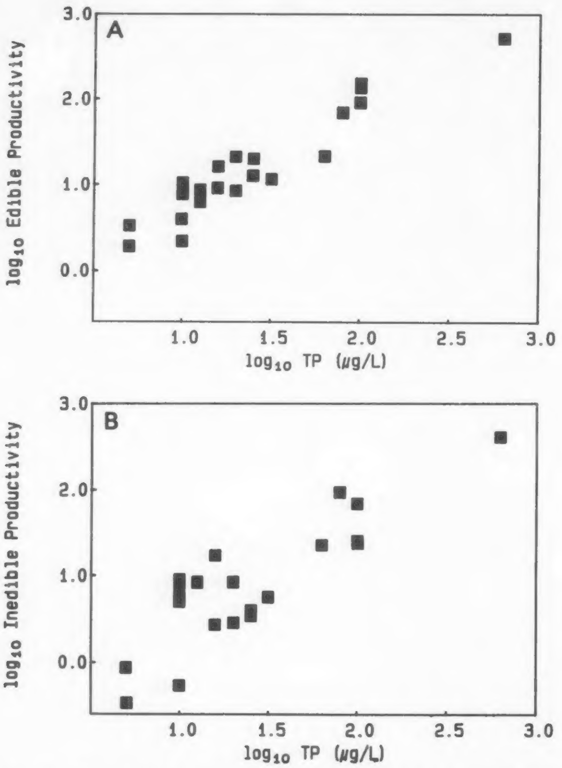

FIG. 3. Relationship between mean summer TP and (A) edible and (B) inedible primary production (g $C \cdot m^{-3} \cdot yr^{-1}$). Data were taken from the following lakes: Chester Morse (Welch et al. 1975), Erie (Munawar and Munawar 1981), Findlay (Welch et al. 1975), Hertel (Kalff 1972), Huron (Munawar and Munawar 1981), Kinneret (Pollingher and Berman 1982), Memphremagog (Watson 1979), Ontario (Munawar and Munawar 1981), Sammamish (Welch et al. 1975), Superior (Munawar and Munawar 1981), Trummen (Gelin and Ripl 1978), and Vombsjön (Gelin 1975).

1981 (Table 2)). Second, of the four regressions, only summer edible biomass has a significantly different relationship with TP.

Production of size-classes along gradients of phosphorus — The production rates of both edible and inedible fractions show highly significant correlations with phosphorus (Table 1; Fig. 3). The slopes of the two equations were not significantly different (*t*-test; $P > 0.05$).

There are two ways of testing whether the ratios of edible and inedible production and biomass vary differently with nutrient levels with our two datasets. Unfortunately, direct comparisons (i.e. using observations from lakes that have complete data on TP, production, and biomass of net- and nanoplankton) are inadequate because there are data available from only a small number of lakes ($n = 4$), and these lakes cover a very restricted range of TP (0.8–1.3 log units). But indirect comparisons are possible. If we assume that both Datasets I and II are representative sample populations, then the slopes from the equations estimating production (e.g. Equations 4 and 5; Table 1) and biomass (Equations 1 and 2; Table 1) for the two groups allow us to compare how the ratios of edible and inedible production to biomass change with enrichment.

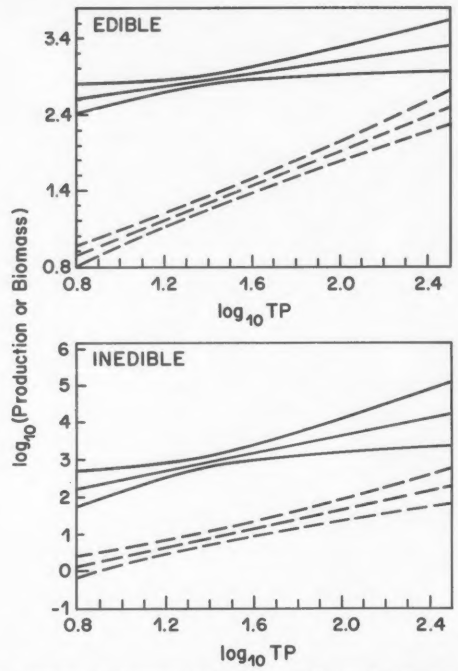

FIG. 4. Changes in biomass (solid lines, µg/L) and primary production (broken lines, g $C \cdot m^{-3} \cdot yr^{-1}$) for edible and inedible fractions based on regression equations (Table 1). The regression lines and 95% confidence intervals for mean prediction are presented.

Figure 4 shows the relationships between TP and mean production and biomass, with the 95% prediction intervals, for the two groups. There is a disproportionate increase in the production of the edible group in relation to its biomass along the TP gradient (i.e. reflected by the increased difference between the predicted averages), while the difference between mean inedible production and biomass does not change (Fig. 4). Therefore, the indirect comparison based on predicted means indicates that ratio of production to biomass for the edible group changes with enrichment, while that of the inedible group does not. Such a trend might be expected if the relative grazing pressure on the edible group does not change with nutrient levels.

Production measurements should be interpreted with caution, especially when using data from a number of sources. Differences in technique may introduce considerable error (e.g. Peterson 1980). In an extensive review of the subject, Stockner and Antia (1986) identify a number of methodological artifacts (e.g. mesh size, filter type, volume filtered, and filtration vacuum applied) which may influence estimates of the production of algal size fractions. However, since these factors varied among studies, we argue that their effects are equivocal and more likely to generate random variability rather than any specific bias: multivariate analysis showed that differences among authors did not account for a significant amount of the total variance in net- or nanoplankton production ($P > 0.05$; df = 20). It is unlikely therefore that size-dependent methodological artifacts produced the approximately 2.5-fold difference in the relationships between TP and the production and biomass of the two size fractions (Fig. 4).

In the introduction, we outlined two alternative mechanisms to explain why algal community structure shifts to a predominance of inedible algae with phosphorus enrichment. The first explanation considered changes in competitive ability of nutrient-limited populations along gradients of enrichment. If the ratios of production to biomass are indicative of underlying specific growth rates, then observations from lakes do not support explanations based on changes in competitive ability between the edible and inedible groups. Our evidence indicates that inedible algae gain no advantage over the edible group throughout the range of TP we examined (i.e. TP < 1000 μg/L). In contrast, patterns in the ratios of production and biomass for the edible and inedible group with TP are consistent with the second hypothesis that herbivores regulate the biomass of the edible group, and therefore largely determine the distribution of biomass between the two groups. Additional support comes from the observations that while there is no apparent relationship between the average biomass of nanoplankton and zooplankton among lakes of different trophy (Hillbricht-Ilkowska et al. 1979; Sprules and Munawar 1986), enrichment increases the biomass of the herbivore community (McCauley and Kalff 1981; Hanson and Peters 1984). Nevertheless, our results indicate that dynamic coupling between edible phytoplankton and their herbivores may not be complete, or parameters of the interaction may change with enrichment. Predator–prey theory (e.g. McCauley et al. 1988) predicts that there should be no increase in the steady state of edible algal biomass with enrichment, despite increases in per capita growth rates. However, the existence of the weak positive relationship between edible algae and TP suggests that other factors may influence the predator–prey interaction. McCauley et al. (1988) have examined this for natural predator–prey systems in which food limitation of herbivores is apparent (Murdoch and McCauley 1985; McCauley and Murdoch 1987). They showed that equilibrium predictions for a series of predator–prey models can predict qualitative variation in the average abundance of *Daphnia* and their algal prey among lakes through realistic variation in parameters of the predator–prey interaction. Clearly, changes in the species composition of the fish community could influence the interaction between herbivores and phytoplankton (Carpenter et al. 1985; Dorazio et al. 1987).

While we have attempted to model changes in phytoplankton communities in terms of their functional size classes, other authors have taken a taxonomic approach. In vitro measurements of differential nutrient uptake and utilization have been used to predict shifts in algal taxonomic groups in the field with some success (e.g. Tilman et al. 1982), while the relative contribution of different groups has been empirically related to nutrient and light levels (Nicholls 1978; Kalff and Watson 1986; Smith 1986). However, a significant amount of variation in taxonomic composition remains unexplained. We suggest that size structure and taxonomy can be combined to improve our ability to explain changes in phytoplankton community structure. The outcome of phytoplankton competition is determined by factors affecting both growth and mortality rates. Our results suggest that within the edible fraction, grazing losses play an extremely important role in regulating edible biomass. If grazing pressure is independent of taxonomy within this fraction (Gliwicz 1977; McCauley and Downing 1985), among-lake differences in the relative contribution of taxonomic groups to edible biomass allow us to better understand and predict nutrient-related taxonomic changes.

In summary, increasing nutrient levels are accompanied by higher edible and inedible algal production rates. This increased production results in a higher inedible biomass and an increased food supply for the herbivorous zooplankton population. This, in turn, is manifested in higher grazer biomass, but little net change in edible algal biomass. Thus, it appears that the interaction between grazers and enrichment largely determines the systematic variation among lakes in the distribution of biomass between major size classes of phytoplankton.

Acknowledgements

This work was supported by a Natural Sciences and Engineering Research Council of Canada operating grant to E. McCauley. We would like to thank Dr. D. Scavia, Dr. V. Smith, Dr. J. Stockner, and an anonymous reviewer for their helpful comments.

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Potential Fishery for Lake Sturgeon (*Acipenser fulvescens*) as Indicated by the Returns of the Hudson's Bay Company Lac la Pluie District

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Holzkamm, T., and M. McCarthy. 1988. Potential fishery for lake sturgeon (*Acipenser fulvescens*) as indicated by the returns of the Hudson's Bay Company Lac la Pluie District. Can. J. Fish. Aquat. Sci. 45: 921–923.

The isinglass returns for the Hudson's Bay Company Lac la Pluie District have been used to estimate the Ojibway harvest of lake sturgeon (*Acipenser fulvescens*) from 1823 to 1885. The majority of these fish were taken in the Rainy River from spawning runs originating in Lake of the Woods. American commercial fishing of sturgeon in Lake of the Woods began in 1888, with commercial operations on the Canadian side following within a few years. Initially high production levels characterize the non-Ojibway fishery for the first 20 yr, with rapid declines due to depleted sturgeon populations in the following years. Similar responses to commercial sturgeon fishing in other areas have led many to conclude that fisheries stocks could not support a significant sustained commercial fishery. In contrast, the Ojibway harvest during 63 yr of fur trade records indicates potential for a substantial sustained commercial sturgeon harvest from the Lake of the Woods basin. The same conclusion is not evident from American and Canadian records of sturgeon harvests from the same drainage basin.

Les revenus enregistrés par la Compagnie de la Baie d'Hudson pour la vente de l'ichtyocolle provenant du district du lac à la Pluie ont servi à l'estimation des captures d'esturgeon de lac (*Acipenser fulvescens*) réalisées par les Ojibwas de 1823 à 1885. La plus grande partie des esturgeons, provenant de remontées naissant dans le lac des Bois, ont été capturés dans la rivière à la Pluie. La pêche commerciale américaine de l'esturgeon dans le lac des Bois a débuté en 1888; l'exploitation commerciale sur le territoire canadien a commencé quelques années plus tard. Au cours des 20 premières années, la pêche par les non-autochtones a été caractérisée par des niveaux élevés de production suivis d'une baisse rapide au cours des années suivantes à cause d'un appauvrissement des populations d'esturgeons. Des réactions semblables des populations à la pêche commerciale dans d'autres régions ont mené plusieurs chercheurs à formuler la conclusion que les stocks ne pouvaient alimenter une pêche commerciale soutenue importante. Par contre, l'exploitation effectuée par les Ojibwas telle que montrée par les données sur le commerce des fourrures couvrant une période de 63 ans révèle qu'il existe un potentiel pour une importante pêche commerciale soutenue dans le bassin versant du lac des Bois. Les données canadiennes et américaines sur l'exploitation de l'esturgeon dans le même bassin versant n'étayent toutefois pas la même conclusion.

Received September 16, 1986
Accepted January 29, 1988
(J8941)

Reçu le 16 septembre 1986
Accepté le 29 janvier 1988

Currently the Lake of the Woods drainage basin supports only a limited sturgeon (*Acipenser fulvescens*) fishery. However, for a brief period during the last decade of the nineteenth century and the first two decades of the twentieth century, this area supported a considerable commercial sturgeon fishery until the available stocks were depleted. The rapid depletion of the original stocks led to the conclusion that a substantial sustained sturgeon fishery was unachievable. Furthermore, Schupp and Macins (1977) have suggested that the Indians living on the Lake of the Woods made only limited demands on fishery resources. Reconstruction of the historic Ojibway sturgeon harvest from the isinglass returns of the Hudson's Bay Company (HBC) Lac la Pluie District, which included Lake of the Woods, provides evidence of a sustained sturgeon fishery of considerable size under Ojibway management. Thus the historical data indicate a potential for a viable sustained sturgeon fishery in the Lake of the Woods.

Much of the data in the daily journals, correspondence, and annual reports of the HBC district headquarters are qualitative and of limited use for this study. For example, the daily journals define the season of greatest Ojibway sturgeon fishing activities but do not consistently record the amounts of sturgeon caught. Quantitative information on sturgeon landings had to be gleaned

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TABLE 1. Hudson's Bay Company Lac la Pluie District annual isinglass production (kg) (Source: HBC Archives B.105/d: Lac la Pluie account books and B.239/h: York Factory/Northern Department returns, Provincial Archives of Manitoba, Winnipeg, Man.).

Year	Isinglass	Year	Isinglass	Year	Isinglass
1823	29	1844	1054	1865	643
1824	73	1845	682	1866	847
1825	63	1846	593	1867	625
1826	112	1847	591	1868	609
1827	90	1848	450	1869	787
1828	74	1849	39	1870	590
1829	70	1850	654	1871	605
1830	140	1851	869	1872	521
1831	168	1852	676	1873	485
1832	200	1853	677	1874	384
1833	357	1854	600	1875	693
1834	353	1855	504	1876	463
1835	342	1856	465	1877	734
1836	274	1857	476	1878	597
1837	505	1858	810	1879	453
1838	480	1859	730	1880	363
1839	798	1860	619	1881	363
1840	565	1861	735	1882	272
1841	286	1862	812	1883	622
1842	712	1863	735	1884	380
1843	719	1864	812	1885	520

indirectly from annual HBC district returns which document an extensive trade in isinglass with the Ojibway.

Isinglass is a high-quality form of gelatin obtained from the swim bladders or sounds of sturgeon. It is processed by slitting the bladder, washing it carefully, peeling the inner membrane away, and drying the latter. It is used in the preparation of jellies, for fining beers and wines, and to make a powerful glue.

Estimation of Sturgeon Harvests from Isinglass Returns

Using the quantitative HBC district returns covering the period from 1823 to 1885, the authors have converted HBC isinglass returns into dressed kilogram equivalents for sturgeon (Table 1). This conversion has been made to facilitate comparison with commercial harvest data kept by the Canadian and American governments after 1888. From 1888 to the present, the authors have relied upon Heyerdahl and Smith (1972) for data on non-Ojibway commercial production. Heyerdahl and Smith (1972) relied upon government records for the Canadian side of the lake and a 1942 report by Carlander for the Minnesota side. Additional data from the Canada Sessional Papers (1894, 1895), covering the years 1893 and 1894, were added to Heyerdahl and Smith (1972).

A ratio for the conversion of isinglass to dressed sturgeon was derived from a report by Evermann and Latimer (1911) who obtained data from commercial fishermen on the amounts of dressed sturgeon and the amounts of isinglass harvested from Lake of the Woods between 1888 and 1909. On the basis of these data, the average of the yearly ratios of isinglass to dressed sturgeon was 1:284. In other words, each kilogram of isinglass represented 284 kg of dressed sturgeon.

When members of the Joint Fisheries Commission visited Lake of the Woods in 1894, they determined that the average weight of 675 sturgeon when dressed for shipment (head, tail, fins, and entrails removed) was approximately 11.35 kg (Canada Sessional Papers 1897). Based on this and the data cited above, the ratio of 1 kg of isinglass to numbers of sturgeon would be 1:25. This ratio was used to reconstruct annual harvests (metric tons) in preference to another of 1:22 which has been cited in several reports (Russell 1898; Harkness and Dymond 1961; Scott and Crossman 1973; see also Prince 1905), since it was derived directly from the Lake of the Woods population of sturgeon. The ratio 1:25 which was derived from Evermann and Latimer (1911) is statistically different from the ratio 1:22 cited in other reports (t-test, df = 21 $p < 0.05$).

Estimates of Ojibway sturgeon harvests derived from records of the isinglass trade are probably low. This is due to the small yield of isinglass per sturgeon and the labor involved in processing the swim bladder which probably resulted in the frequent discarding of bladders from small catches or small sturgeon. In addition, some of the isinglass may have been reserved by the Ojibway for domestic use (Overholt and Callicott 1982) and would not have been recorded by HBC.

Sturgeon Harvests

Historical reconstruction of the Ojibway sturgeon landings provides information which should be of utility in determining potential sustainable yields for Lake of the Woods. The Ojibway harvest of sturgeon from 1823 to 1885 was estimated to be 8 896 233 kg or an average of 141 210 kg/yr. The non-Ojibway commercial harvest from Lake of the Woods starting in 1888 quickly rose to a high level and then after 1915 collapsed to very low levels so that the total yield of sturgeon estimated over the same number of years as are available for the Ojibway fishery was 6 362 851 kg or an average of only 100 890 kg/yr (Fig. 1).

There is a brief decline in HBC isinglass returns following the negotiation of Treaty No. 3 in the 1870s (Fig. 1). This decline may be due to increased emphasis upon agricultural production by the Ojibway during this period. Certainly, full-time farming would have interfered with fishing to an extent not seen during periods of part-time farming. Furthermore, the initial high harvests by non-Indian commercial fishermen in 1888 would indicate that sturgeon were still abundant.

In general, sustained large-scale commercial fisheries for sturgeon have been viewed as unachievable. Prince (1905), Tower (1909), Evermann and Latimer (1911), Carlander (1949), Williams (1951), Eddy and Surber (1960), Harkness and Dymond (1961), and Priegel (1971) have considered the rapid decline of sturgeon fisheries under unrestricted commercial fishing. Harkness and Dymond (1961) have stated that "It is quite certain that nothing approaching the yields obtained when sturgeon were first fished is possible under continuous fishing." According to Priegel (1971): "Unlike other game and panfish species, the lake sturgeon will give only a relatively small, sustained yield. We do not have adequate information to enable us to decide whether, under different management techniques, higher continuous yields than those now being realized could be attained. There is reason to believe that sustained yields larger than those now being attained in waters where conditions are still essentially primitive are not possible."

Reconstruction of the Ojibway sturgeon harvest from HBC isinglass returns contradicts such views. Sturgeon are a long-lived fish which continue to grow throughout their lives, attaining considerable size (90 kg or more) (Scott and Crossman 1973). The small average size of the Lake of the Woods sturgeon (11.35 kg dressed) (Canada Sessional Papers 1897) taken early in the non-Ojibway commercial fishing period suggests that the population was already being heavily harvested.

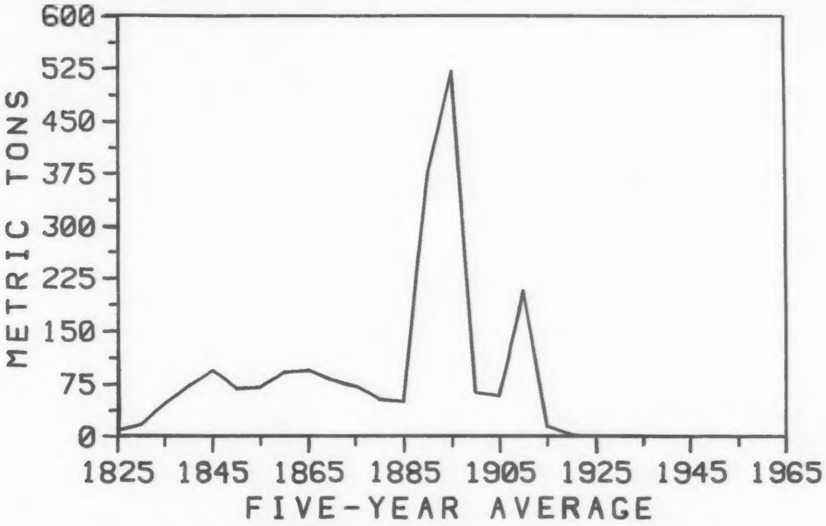

FIG. 1. Lake of the Woods sturgeon harvest from 1825 to 1964.

Subsistence was the primary motivation for Ojibway sturgeon fishing during the nineteenth century, and isinglass was a significant commercial byproduct. In the years following the signing of Treaty No. 3, subsistence harvesting by white settlers added to the pressure on the sturgeon population. The subsistence activities of both Ojibway and white settlers continued after the commencement of non-Ojibway commercial fisheries in 1888.

Apparently, the combined impact of all of the demands upon the sturgeon fishery resulted in its destruction. However, reconstruction of Ojibway sturgeon landings from the HBC Lac la Pluie District isinglass returns indicates the potential for a sizable sturgeon fishery. It is hoped that long-term management plans for the Lake of the Woods fishery will include provision for the restoration of a valuable resource which once produced a sustained yield of considerable size.

Acknowledgments

The authors wish to thank the Hudson's Bay Company Archives and Grand Council of the Ojibways, Treaty No. 3, for permission to use their collections. Furthermore, we would like to thank Chief Willie Wilson and other members of the Manitou Rapids Band for sharing their knowledge of the Rainy River fisheries with us.

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L'Institut a le plaisir d'annoncer que le professeur Curt Forsberg, directeur de l'Institut de limnologie de l'Université d'Uppsala (Suède) prononcera, à l'INRE, la conférence inaugurale Vollenweider au début de juin 1988. On veut ainsi reconnaître les découvertes du professeur Forsberg relatives à la diminution de l'eutrophisation, ses travaux de pionnier sur le rétablissement des lacs acidifiés et son excellence de leader dans la recherche sur la limnologie en Scandinavie.

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CJFSDX45(5) 757–925 (1988)
ISSN 0706-652X

Subscription rates/Abonnements

Canada: Institutional/Collectif $170; Personal/Personnel $65
Other countries/Autres pays : Institutional/Collectif $204; Personal/Personnel $78
Single issue/Par numéro : $12.95 (Canada); $15.55 (Other countries/Autres pays)